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Biological Characteristics of Coastal Populations of Sockeye Salmon (*Oncorhynchus nerka*) in British Columbia

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BIOLOGICAL CHARACTERISTICS OF COASTAL POPULATIONS OF SOCKEYE SALMON (*Oncorhynchus nerka*) IN BRITISH COLUMBIA

by

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ABSTRACT

Rutherford, D. T., C. C. Wood, K. D. Hyatt, L. Margolis, T. McDonald, B. E. Riddell, and R. E. Withler. 1992. Biological characteristics of coastal populations of sockeye salmon (*Oncorhynchus nerka*) in British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1849: 47 p.

Mature sockeye salmon (*Oncorhynchus nerka*) inhabiting 28 lakes along the British Columbia coast were examined to document variation in life histories and biological characteristics that might prove useful as "markers" for stock identification. Age and length composition, scale pattern characteristics, and prevalence of the brain parasite *Myxobolus neurobius* were highly variable among stocks. Freshwater growth of sockeye (inferred from scale patterns) tended to be slower in coastal lakes than in a typical interior type lake. Electrophoretic variation among populations was detected at 14 loci of the 32 examined but only nine loci were polymorphic such that the frequency of the common allele was < 95%. Simulations with a maximum likelihood mixture model indicated that biochemical genetic, brain parasite and freshwater age markers could be used in combination to distinguish most stocks but not all. Stock composition estimates for Mercer Lake (the most unique population) were very reliable (bias < 5%, standard deviation < 6%), whereas those for Koeye Lake (one of the least unique populations) were much less reliable (bias > 40%, standard deviation > 16%).

RÉSUMÉ

Rutherford, D. T., C. C. Wood, K. D. Hyatt, L. Margolis, T. McDonald, B. E. Riddell, and R. E. Withler. 1992. Biological characteristics of coastal populations of sockeye salmon (*Oncorhynchus nerka*) in British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1849: 47 p.

Le saumon rouge adulte (*Oncorhynchus nerka*) de 28 lacs situés le long de la côte de la Colombie-Britannique a été examiné afin d'obtenir des données sur la variation du cycle biologique et les caractéristiques biologiques qui pourraient se révéler utiles comme "marqueurs" (indices) à des fins d'identification des stocks. La composition par âges et par longueurs, les caractéristiques de la structure des écailles et la fréquence de *Myxobolus arcticus*, un parasite du cerveau, étaient très variables d'un stock à l'autre. La croissance en eau douce du saumon rouge (déduite de la structure des écailles) avait tendance à être plus lente dans les lacs côtiers que dans les lacs typiques de l'intérieur. On a détecté une variation électrophorétique entre les populations sur 14 des 32 loci examinés, mais seulement 9 loci étaient polymorphes de sorte que la fréquence de l'allèle commun était inférieure à 95 %. Des simulations à l'aide d'un modèle mixte du maximum de vraisemblance ont révélé que les indices relatifs au génie biochimique, au parasite du cerveau et au rythme de croissance en eau douce peuvent être utilisés conjointement pour établir des distinctions entre la plupart des stocks. Les estimations de la composition des stocks de lac Mercer (la population la plus unique) étaient très fiables (biais <5 %, écart-type <6 %), tandis que celles du lac Koeye (l'une des populations les moins uniques) étaient beaucoup moins fiables (bias >40 %, écart-type >16 %).

INTRODUCTION

Sockeye salmon (*Oncorhynchus nerka*) are known to inhabit a large number of lakes along the Pacific coast of Canada which are not part of the large river systems of the Taku, Stikine, Nass, Skeena or Fraser watersheds (Aro and Shepard 1967). These "coastal sockeye" typically migrate less than 50 km upstream from the sea to spawn and spend their freshwater life in extremely oligotrophic and warm-monomictic nursery lakes. Because of the wet coastal climate, water residence times in coastal lakes are shorter, phosphorus concentrations are lower, and food chains leading to juvenile sockeye are longer than in interior lakes inhabited by sockeye (Hyatt and Stockner 1985; Stockner 1987).

In this report, we document the variation in biological characteristics of mature sockeye collected from 28 coastal populations. The characters examined include length and age at maturity, age at smolting, scale patterns, prevalence of the myxosporean parasite *Myxobolus arcticus*, and allele frequencies at up to 32 loci. Where possible, we make inferences about the biology and productivity of these coastal populations by considering their life histories and rates of growth in fresh water, especially in comparison to sockeye from Shuswap Lake in the Fraser River, a fairly typical interior lake.

Biological characteristics which vary among salmon stocks can often be used as natural "markers" for stock identification (e.g. Henry 1961, scales: Fukuhara et al. 1962, morphology: Margolis 1963, parasites: Child 1980, protein electrophoresis). Wood et al. (1988, 1989) have previously demonstrated the feasibility of using freshwater age, *Myxobolus arcticus* (as *M. neurobius*) prevalence, scale pattern, and allele frequency data in combination to estimate the stock composition of sockeye catches in mixed-stock fisheries. We employed similar techniques using data presented in this report to assess the potential for differentiating coastal sockeye populations.

METHODS

COLLECTION OF SAMPLES FROM SPAWNING SITES

Live sockeye were collected from 28 coastal lakes spread over a wide geographic area (Fig. 1). To facilitate comparison among stocks we grouped our collections into four geographic regions. We defined these regions as: (i) Queen Charlotte Islands (populations 1-6, statistical areas 1&2); (ii) northern (populations 7-15, statistical areas 5-7 and Taku); (iii) central (populations 16-20, statistical areas 8-10); (iv) southern (populations 21-28, statistical areas 11-24). At most sites live sockeye were collected using tangle nets with a 110-mm mesh. However a 33 X 2-m beach seine was used at Devon, Hobiton, Kennedy, and Woss lakes, and gaffs and pews

were used in 1984 at Long and Owikeno lakes. The 1982 Long and 1983 Bonilla Lake samples were collected at weirs, the Sproat and Great Central Lake samples at fishways. Kennedy and Hobiton lakes were the only two sites where samples were taken from spawning areas along the lake shore. In general, sites were sampled only once over a period of 1 - 2 days during peak spawning activity (Table 1). However, some sites were sampled either before or after the peak spawning period owing to annual variation in spawning time and factors restricting access (e.g., weather and geography).

SAMPLING PROCEDURES

Most fish were sampled in the field for postorbital-hypural length, sex, scales, otoliths, brain (to examine for the parasite *Myxobolus arcticus*) and the following tissues for electrophoretic analysis; heart, liver, eyeball and skeletal muscle (Table 1). All fish were alive when captured and tissues were frozen within 4-8 h of death to preserve enzyme activity. Some tissue samples were frozen immediately in liquid nitrogen whereas others were frozen in domestic freezers. Forceps and knives were wiped and rinsed carefully after sampling each fish to avoid contaminating subsequent specimens with *Myxobolus* spores. Otoliths were stored in trays containing a glycerine/water solution. Scales were mounted on gummed cards.

SCALE AND OTOLITH ANALYSIS

Age was determined from the surface of otoliths as described by Bilton and Jenkinson (1968). Otolith ages were used to interpret scale growth zones because it was rarely possible to determine total age from scales alone owing to resorption of the scale margins in spawning fish.

Six scale pattern measurements were recorded for the two dominant age classes in samples (age 1.2 and 1.3). These patterns included the number of circuli (NC_i) and incremental distances or widths (ID_i) within each of the three growth zones representing the first year's growth in fresh water (i=1), "spring" or "plus" growth in fresh water during the second year prior to entering the sea (i=2), and marine growth during the remainder of the second year (i=3). The number of circuli (NC) and the incremental distances (ID) between circuli within growth zones along the anterior-posterior axis (Fig. 2) were measured from projected images at 100 X magnification using a computerized digitizing tablet. Incremental distances were measured between inside edges of circuli. Scale pattern measurements from brood years affected by nutrient enrichment by the Lake Enrichment Program (Stockner 1987) were documented but excluded from analyses.

To compare growth rates of juvenile sockeye in coastal lakes to those in a typical interior type lake (Shuswap Lake), circulus counts in zone 1 were plotted against fish density. Again, nutrient enriched lakes were

excluded. Circulus counts and limnetic fish densities for Shuswap lake were taken from Williams et al. (1989); juvenile fish densities in coastal lakes were estimated following the procedure outlined in Hyatt et al. (1984).

PARASITE EXAMINATION

Brains were examined for the presence of the parasite *Myxobolus arcticus* by digesting the brain in a pepsin-hydrochloric acid solution for 3-5 h. The sediment, following centrifugation, was examined at 350 x using a compound microscope, for the presence of spores. Parasite prevalence refers to the proportion of brain samples containing the parasite. The intensity of infection within individual fish was not evaluated.

ELECTROPHORETIC ANALYSIS

Tissues were stored at approximately -20°C and later analyzed by horizontal starch gel electrophoresis as described by Utter et al. (1983). Electrophoretic variation was assayed at 32 loci (Table 2) which exhibit simple Mendelian segregation. Nine of these were duplicate loci (e.g. *sMDH-1, 2**) which could not be scored individually; accordingly, these will be treated as if they were single loci. A locus was considered polymorphic if the frequency of the most common allele was < 0.95. Alleles and loci are designated using the nomenclature proposed by Shaklee et al. (1990).

Allele frequencies were computed by summing alleles across all genotypes and dividing by the total number of alleles (2n). Genotype frequencies at each locus were examined for departure from Hardy-Weinberg equilibrium by chi-square analysis. Genetic structuring of sockeye stocks sampled was analyzed by comparing gene diversity among the four geographic regions and among sites within each region using the standardized genetic variance statistic (F_{ST}) (Wright 1965; Chakraborty 1980). A dendrogram of genetic similarity was constructed using unbiased genetic identities (Nei 1978) and the unweighted pair group method (Sneath and Sokal 1973). This dendrogram was based on all 11 loci screened in each sample (*PGM-1**, *PGM-2**,*sMDH-3,4**, *GPI-1**, *MEP-1**, *G6PDH**, *sIDHP-3,4**, *G3PDH-1**,*sMDH-1,2**, *LDH-D**, *LDH-C**). Another dendrogram of cumulative differences in gene frequencies, *Myxobolus* prevalence, and freshwater age composition was constructed using the log likelihood ratio distance (Wood 1989) to reflect the potential for differentiating individual stocks using all markers in combination.

SIMULATIONS

To evaluate the reliability of stock composition estimates under ideal conditions, Monte Carlo simulations were performed following the general procedures outlined by Wood et al. (1987, 1989). Three mixture types of known composition were analyzed; each mixture sample included 300 fish from a single stock to highlight potential misclassifications. The contributing stocks were selected to provide a range from easy to difficult mixture problems as judged from the dendrogram of cumulative differences. Three mixtures were created. Mixture 1 included only fish from Mikado Lake; mixture 2, from Long Lake; and mixture 3 from Mercer Lake. The biological markers used in the simulations were; freshwater age, prevalence of the brain parasite *Myxobolus arcticus*, and the five most polymorphic loci: *PGM-1**, *PGM-2**, *LDH-D**, *sMDH-3,4**, *sIDHP-3,4**. Scale patterns were not used because they often vary from year to year (Wood et al. 1988, 1989) and it was not possible to collect scale samples from all stocks in a single year.

Mixture composition was estimated using the maximum likelihood method of Fournier et al. (1984). Means and standard deviations were calculated from the 100 estimates for each of the three mixtures. We refer to the difference between the mean estimate of the proportion contributed by a selected stock and its true contribution (1.00) as the "mean error" for that stock. The mean error and standard deviation statistics reflect bias and imprecision, respectively, for estimates of mixing proportions of particular stocks.

RESULTS

AGE COMPOSITION

Freshwater age composition varied significantly among spawning sites ($p<0.005$, ANOVA). Age 1. fish were most abundant in all but one sample and proportions ranged from 0.40 to 1.00 among the stocks sampled (Table 3, Fig. 3). Generally age 2. spawners were more abundant in the northern and Queen Charlotte Island regions (#1-15, mean = 22%) than in southern and central regions (#16-28, mean = 5%) ($p<0.001$, likelihood ratio χ^2). Age 2. spawners were dominant in two lakes (Mikado, 60% age 2. and Mercer, 53% age 2.) and uncommon (<5%) in only four lakes (Border, Awun, Lowe, and Yakoun) in the northern and Queen Charlotte Island regions. In contrast, age 2. spawners were uncommon in 10 of the 13 lakes sampled in the central and southern regions (Table 3).

LENGTH DISTRIBUTION AND SEX RATIO

Post-orbital hypural length varied significantly among spawning sites in the northern, central, and southern regions ($P<0.020$, ANOVA). Matching length, sex, and age data were only available for two stocks in the Queen Charlotte Island region and only the age 1.2 females were significantly different between the two stocks ($P<0.001$, ANOVA). Skidegate and Cheewhat Lake samples included the smallest fish at age 1.2. The Lowe Lake sample included the largest fish for both the 1.2 and 1.3 age classes but considerable overlap existed in the length distributions among the samples (Table 4, Fig.4). Regional differences in length were also observed ($P<0.001$, ANOVA). The smallest sockeye tended to occur in the Queen Charlotte Island region, the largest, in the northern region.

Sex ratio ranged from 14-76% female among the samples (Table 5). This variation in sex ratio probably arises for two reasons: first, sex ratios sometimes change throughout the spawning period (Lorz and Northcote 1965; McCart 1970) and not all stocks were sampled at the time of peak spawning activity; and second, the sampling gear tended to select males over females because the large teeth and hooked snouts of males increased their probability of entanglement in nets.

SCALE PATTERNS

Scale pattern data are summarized by age group and growth zone for all spawning locations (Table 6, 7). Circuli counts and scale zone widths for age 1.2 and 1.3 fish are illustrated in Figure 5 to facilitate comparison among stocks. Mean circuli counts for NC_1 range from 6.77-14.40 and 7.61-13.87 for age 1.2 and 1.3 fish, respectively. The two most northern regions (Queen Charlotte Islands and northern) tended to have higher circulus counts and widths for zone 1 than those of the central and southern region ($p<0.001$, ANOVA). For the 1.2 age class Canoona lake sockeye had the highest number of circuli (NC_1=12.92) and the greatest scale zone width (ID_1=35.83). No age 1.3 fish were sampled from Canoona Lake. Of stocks containing the 1.3 age class, Banks Lake sockeye had the highest number of circuli (NC_1=12.67) and the greatest scale zone width (ID_1=34.69). Sockeye from Koeye and Tenas lakes had the least number of circuli (NC_1=6.62 and 7.61) for ages 1.2 and 1.3, respectively. Koeye and Woss had the smallest scale zone width (ID_1=18.25 and 19.83) for age 1.2 and 1.3, respectively. Variability among age classes within lakes was large in some populations. For example, mean zone 1 circulus counts (NC_1) in Koeye lake sockeye varied from 6.62 to 13.87 for age 1.2 and 1.3 fish, respectively; scale zone widths (ID_1) also varied from 18.25 to 34.72, respectively. Only Mikado Lake sockeye showed no significant variation between age classes in circulus counts for scale zones 1 and 2.

The coastal lake circulus counts (NC_1) were highly correlated with juvenile limnetic fish density ($r=-0.78$). This is because circulus counts are a good index of juvenile growth rate (Clutter and Whitesel 1956; Bilton and

Smith 1969; Goodlad et al. 1974; Fisher and Pearcy 1990), and because juvenile growth rates are depressed at high density owing to intraspecific competition (Brocksen et al. 1970). The relationships between circulus counts and fish density for coastal lakes versus a typical interior type lake (Shuswap Lake) indicate that conditions for sockeye growth are less favourable in coastal lakes than in Shuswap Lake (Fig. 6).

PARASITE PREVALENCE

The prevalence of the myxosporean parasite *Myxobolus arcticus* ranged from 0-100% among the stocks sampled (Table 8, Fig. 7). This parasite was absent in six sampling locations: Awun, Yakoun, Kitlope, Kimsquit, Skidegate, and Long lakes. The 1990 sample from Great Central Lake was unusual because it indicated a *Myxobolus* prevalence of 18%; the highest rate previously reported for this stock was 8% (Quinn et al. 1987). The Woss, Lowe, and Mathers samples exhibited an intermediate prevalence of 55, 41, and 40%, respectively. All other stocks sampled had a parasite prevalence of greater than 80%. No obvious regional differences were observed in parasite prevalence. ($p>0.20$, likelihood ratio χ^2).

ELECTROPHORETIC VARIATION

Nine of the 32 loci examined by electrophoresis were polymorphic to the extent that the common (100) allele frequencies were less than 0.950 (Table 9). These were *PGM-1**, *PGM-2**, *sMDH-3,4**, *G6PDH**, *LDH-D**, *sIDHP-3,4**, *MPI**, *PEPA**, *ALAT**. Average heterozygosities over the 32 loci ranged from 0.009 to 0.067. Among populations sampled, eight of the 102 chi-square tests for deviation of the observed genotypic frequencies from the expected Hardy-Weinberg genotypic frequencies were statistically significant at the 5% critical value. Three of these were significant after adjusting for multiple comparisons ($\alpha=0.0005$).

As expected, replicate samples from different years were genetically similar (Fig. 8). The Devon and Mikado lakes stocks are less than 5 km apart and also appear to be genetically very similar to one another, however; the standardized genetic variance of allelic frequencies (F_{ST}) among populations was 0.167 implying that 17% of the total genetic variation was among populations and 82% originated within populations. Variation among regions was 1%.

SIMULATION RESULTS

Simulation experiments to estimate the stock composition of mixtures of known composition using the maximum likelihood procedures described by Wood et al. (1989) demonstrated that these biological markers can be used to differentiate many of the sockeye populations described in this report. Of the three populations compared, the Koeye Lake population was predicted to be the most difficult stock to distinguish based on the dendrogram (Fig. 9). Estimates of composition of a test mixture composed only of Koeye sockeye were unreliable; the mean estimated proportion was only 56% (bias=44%,SD=17%) (Fig. 10). In contrast, the Mercer Lake population was distinguished with greater reliability (bias<4%, SD<6%), and the Long Lake population with intermediate reliability (bias<12%, SD<12%) as predicted from the dendrogram.

DISCUSSION

The coastal sockeye populations studied in this report exhibit substantial differences in terms of size and age at maturity, parasite prevalence and juvenile growth rate. These differences are surprising given that the lakes which these sockeye inhabit as juveniles are quite homogeneous with respect to extremely low phosphorus concentrations (1-3 μg $TP \cdot L^{-1}$), and extreme oligotrophic conditions (avg 1-4 μg $Tchl\text{-}L^{-1}$). The majority of lakes are warm-monomictic and range from 13 to 212 m in mean depth and from 1.8 to 51 km^2 in surface area (Hyatt and Stockner 1985).

Variations in size and age at maturity may result both from short term variations in environmental conditions encountered by a given generation of fish and from long term adaptation to unique features in each lake system. For example, variation in adult body size is commonly viewed as adaptive to local conditions (Healey 1987; Holtby and Healey 1986).

Extreme differences in body size at maturity among some stocks in this study probably reflect adaptations for migration to the spawning grounds. Salmon of large body size can surmount hydraulic conditions that are clearly barriers to smaller fish (Godfrey et al. 1954). At Lowe Lake, adult sockeye must surmount Verney Falls (3m high) in order to reach their spawning area whereas at Cheewhat Lake, adult sockeye face few, if any, hydraulic barriers. The Cheewhat River has such a low gradient that Cheewhat Lake itself is influenced by tidal action. Thus, differences in the difficulty of upstream migration may explain why: (1) Lowe Lake sockeye exhibited the largest size at age (age 1.2 average 543 cm; age 1.3 average 556 cm) whereas Cheewhat sockeye exhibited one of the smallest sizes at age (age 1.2 average 370 cm) of all the sockeye populations considered in this report; and (2) small, age 1.1 adults ("jacks") were absent from Lowe Lake samples but accounted for a relatively large proportion of Cheewhat sockeye.

Fresh water age was also highly variable among our samples but we did see some indication of a north-south cline in the occurrence of age 2. fish (Fig. 3). *Myxobolus arcticus* prevalence and allozyme allele frequencies varied among stocks but not according to any recognizable pattern. The unusually high *Myxobolus arcticus* prevalence of 18% in the 1990 sample from Great Central Lake probably resulted from straying from the nearby Sproat Lake stock which has a high prevalence of infection by this parasite. Sproat and Great Central Lake sockeye share a common migration route up the Somass River before entering the Sproat and Stamp rivers which drain Sproat and Great Central lakes, respectively. Straying between Sproat and Great Central lake populations is typically very low (<1%, Quinn et al. 1987). However, during the adult migration in 1990, water flow in the Sproat River was unusually low and water temperatures high making this river unfavourable to migrating sockeye and resulting in abnormally high mortality (W. Luedke Dept. of Fisheries and Oceans, 3225 Stephenson Pt. Rd. Nanaimo, B.C. V9T 1K3).

Circulus counts indicated that freshwater growth was density dependent in coastal sockeye populations, as reported for other sockeye populations (Foerster 1968; Goodlad et al. 1974; Hyatt and Stockner 1985). Factors affecting juvenile sockeye density were not examined in this study, but it is apparent that large variations in sockeye fry density occur among coastal lakes. After accounting for the effects of limnetic fish density, juvenile growth rate, inferred from circulus counts, was lower in coastal lakes than in a typical interior lake. This finding is consistent with conclusions from previous studies (Stockner 1987; Stockner and Shortreed 1989) that lake productivity is generally lower for coastal lakes than for the large lakes of the British Columbia interior.

There is considerable evidence that the allele frequencies of the allozymes studied and the prevalence of *Myxobolus arcticus* infections are stable over time (Beacham et al. 1988; Wood et al. 1988, 1989; Moles et al. 1990; Winans and Helle 1991). However, it is not known whether observed differences in biological traits such as size and age at maturity are genetically determined and would persist over time because only a few populations were sampled in more than one year. Genetic-environmental interactions may explain most of the differences between years observed for these stocks. For example, large variations in fry density from year to year would tend to alter juvenile sockeye growth rate which is known to influence the size and age, of sockeye smolts at seaward migration (Foerster 1968; Koenings and Burkett 1987). Size and age at seaward migration may in turn influence size, age, and sex ratios of adults returning in a given calendar year (Bilton 1980; Hyatt and Stockner 1985; Bradford and Peterman 1987).

The substantial variation that exists among coastal sockeye salmon stocks with respect to freshwater age composition, scale patterns, prevalence of the brain parasite *Myxobolus arcticus*, and allele frequencies at the five most polymorphic loci is potentially useful for stock identification. In practice, other larger interior sockeye populations would probably also be represented in any mixed stock fishery involving these coastal populations. Thus, our ability to differentiate these stocks would depend on the biological attributes of stocks not considered here. Nevertheless, this simulation study is a first step in determining the potential utility of these markers; if

stock composition estimates were unreliable at this stage, then practical application of this approach would be futile.

In conclusion, the surprising degree of variability observed among these populations precludes any attempt to describe the biological attributes of a "typical" coastal sockeye population. In a sense, coastal populations are characterized by their diversity of life history types and by the low productivity of their juvenile rearing habitat. This variability could be used to advantage for improving the estimation of contributions from these stocks to catches in mixed stock fisheries.

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REFERENCES

Aro, K. V., and M. P. Shepard. 1967. Pacific salmon in Canada. Salmon of the North Pacific Ocean - Part IV. Spawning populations of North Pacific Salmon. Int. North Pacific Fish. Comm. Bull. 23: 225-327.

Beacham, T. D., R. E. Withler, C. B. Murray, and L. W. Barner. 1988. Variation in body size, morphology, egg size, and biochemical genetics of pink salmon in British Columbia. Trans. Am. Fish. Soc. 117: 109-126.

Bilton, H. T. 1980. Returns of adult coho salmon in relation to mean size and time at release of juveniles to the catch and the escapement. Can. Tech. Rep. Fish. Aquat. Sci. 941: 41 p.

Bilton, H. T., and D. W. Jenkinson. 1968. Comparison of otolith and scale methods for aging sockeye (*Oncorhynchus nerka*) and chum (*O. keta*) salmon. J. Fish. Res. Board Can. 25: 1067-1069.

Bilton, H. T., and H. D. Smith. 1969. Scale characteristics of sockeye salmon (*Oncorhynchus nerka*) originating from small nursery areas of the Skeena River system. Can. Tech. Rep. Fish. Aquat. Sci. 133: 33 p.

Bradford, M. J., and R. M. Peterman. 1987. Maternal size effects may explain positive correlations between age at maturity of parent and offspring sockeye salmon (*Oncorhynchus nerka*). p. 90-100. In H. D. Smith, L. Margolis, and C. C. Wood (ed.) Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Brocksen, R. W., G. E., Davis and C. E. Warren. 1970. Analysis of trophic processes on the basis of density-dependent functions. p. 468-498. In J. H. Steele (ed.) Marine food chains. Oliver and Boyd, Edinburgh, Scotland.

Chakraborty, R. 1980. Gene diversity analysis in nested subdivided populations. Genetics 96: 721-723.

Child, A. R. 1980. Identification of stocks of Atlantic salmon (*Salmo salar* L.) by electrophoretic analysis of serum proteins. Rapp. P.-V. Reun. Cons. Int. Explor. Mer. 176: 415-423.

Clayton, J. W., and D. W. Tretiak. 1972. Amine-citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Board Can. 29: 1169-1172.

Clutter, R. I., and L. E. Whitesel. 1956. Collection and interpretation of sockeye salmon scales. Int. Pacific Salmon Fish. Comm. Bull. 9: 159 p.

Fisher, J. P., and W. G. Pearcy. 1990. Spacing of scale circuli versus growth rate in young coho salmon. Fish. Bull. 88: 637-643.

Foerster, R. E. 1968. The sockeye salmon (*Oncorhynchus nerka*). Bull. Fish. Res. Board Can. 162: 422 p.

Fournier, D. A., T. D. Beacham, B. E. Riddell, and C. A. Busak. 1984. Estimating stock composition in mixed-stock fisheries using morphometric, meristic and electrophoretic characteristics. Can. J. Fish. Aquat. Sci. 41: 400-408.

Fukuhara, F. M., S. Murai, J. J. LaLanne, and A. Sribhibhadh. 1962. Continental origin of red salmon as determined from morphological characters. Int. North Pacific Fish. Comm. Bull. 8: 15-109.

Godfrey, H., W. R. Hourston, J. W. Stokes, and F. C. Withler. 1954. Effects of a rock slide on Babine River salmon. Bull. Fish. Res. Board Can. 101: 100 p.

Goodlad, J. C., T. W. Gjernes, and E. L. Brannen. 1974. Factors affecting sockeye (*Oncorhynchus nerka*) growth in four lakes of the Fraser River system. J. Fish. Res. Board Can. 31: 871-892.

Healey, M. C. 1987. The adaptive significance of age and size at maturity in female sockeye salmon (*Oncorhynchus nerka*). p. 110-117. In H. D. Smith, L. Margolis, and C. C. Wood (ed.) Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Henry, K. 1961. Racial identification of Fraser River sockeye salmon (*Oncorhynchus nerka* Walbaum) by means of scales and its application to salmon management. Int. North Pacific Fish. Comm. Bull. 12: 97 p.

Holtby, L. B., and M. C. Healey. 1986. Selection for adult size in female coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 43: 1946-1959.

Hyatt, K. D., D. Rutherford, T. Gjernes, P. Rankin, and T. Cone. 1984. Lake Enrichment Program: Juvenile Sockeye Unit survey guidelines. Can. Manuscr. Rept. Fish. Aquat. Sci. 1796: 84 p.

Hyatt, K. D., and J. G. Stockner. 1985. Responses of sockeye salmon (*Oncorhynchus nerka*) to fertilization of British Columbia coastal lakes. Can. J. Fish. Aquat. Sci. 42: 320-331.

Koenings, J. P., and R. D. Burkett. 1987. Population characteristics of sockeye salmon (*Oncorhynchus nerka*) smolts relative to temperature regimes, euphotic volume, fry density and forage base within Alaskan lakes. p. 216-234. In H.D. Smith, L. Margolis, and C.C. Wood (ed.). Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Lorz, H. W., and T. G. Northcote. 1965. Factors affecting stream location, and timing intensity of entry by spawning kokanee (*Oncorhynchus nerka*) into an inlet of Nicola Lake, British Columbia. J. Fish. Res. Board Can. 22: 665-687.

Margolis, L. 1963. Parasites as indicators of the geographic origin of sockeye salmon (*Oncorhynchus nerka* Walbaum) occurring in the North Pacific ocean and adjacent seas. Int. North Pacific Fish. Comm. Bull. 11: 101-156.

Markert, C. L., and I. Faulhaber. 1965. Lactate dehydrogenase isozyme patterns of fish. J. Exp. Zool. 156: 319-332.

McCart, P. J. 1970. A polymorphic population of *Oncorhynchus nerka* in Babine Lake, British Columbia. Ph.D. thesis, University of British Columbia, Vancouver, B. C.

Moles, A., P. Rounds, and C. Kondzela. 1990. Use of the brain parasite *Myxobolus neurobius* in separating mixed stocks of sockeye salmon. Am. Fish. Soc. Sympos. 7: 224-231.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583-590.

Quinn, T. P., C. C. Wood, L. Margolis, B. E. Riddell, and K. D. Hyatt. 1987. Homing in wild sockeye salmon (*Oncorhynchus nerka*) populations as inferred from differences in parasite prevalence and allozyme allele frequencies. Can. J. Fish. Aquat. Sci. 44: 1963-1971.

Ridgway, G. J., S. W. Sherburne, and R. D. Lewis. 1970. Polymorphism in esterase of Atlantic herring. Trans. Am. Fish. Soc. 99: 147-151.

Shaklee, J. B., F. W. Allendorf, D. C. Morizot, and G. S. Whitt. 1990. Gene nomenclature for protein-coding loci in fish. Trans. Am. Fish. Soc. 119: 1-13.

Sneath, P. H., and R. R. Sokal. 1973. Numerical taxonomy. W. H. Freeman and Co., San Francisco, CA. 573 p.

Stockner, J. G. 1987. Lake fertilization: the enrichment cycle and lake sockeye salmon (*Oncorhynchus nerka*) production. p. 198-215. In H. D. Smith, L. Margolis, and C.C. Wood (ed.) Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Stockner, J. G., and K. Shortreed. 1989. Algal picoplankton production and contribution to food-webs in oligotrophic British Columbia lakes. Hydrobiologia 173: 151-166.

Utter, F. M., P. Aebersold, J. Helle, and G. Winans. 1983. Genetic characterization of populations in the southeastern range of sockeye salmon. p. 17-32. In J. M. Walton and D. B. Houston (ed.) Proceedings of the Olympic Wild Fish Conference. Port Angeles, Washington.

Williams, I. V., P. Gilhousen, W. Saito, T. Gjernes, K. Morton, R. Johnson and D. Brock. 1989. Studies of the lacustrine biology of the sockeye salmon (*Oncorhynchus nerka*) in the Shuswap system. Int. Pacific Salmon Fish. Comm. Bull. 24: 108 p.

Winans, G. A., and J. H. Helle. 1991. Electrophoretic variation in sockeye salmon (*Oncorhynchus nerka*) in Southeast Alaska. Fish. Bull. (in press)

Wood, C. C. 1989. The utility of similarity dendrograms in stock composition analysis. Can. J. Fish. Aquat. Sci. 46: 2121-2128.

Wood, C. C., G. T. Oliver, and D. T. Rutherford. 1988. Comparison of several biological markers used for stock identification of sockeye salmon (*Oncorhynchus nerka*) in northern British Columbia and Southeast Alaska. Can. Tech. Rep. Fish. Aquat. Sci. 1624: 44 p.

Wood, C. C., S. McKinnell, T. J. Mulligan, and D. A. Fournier. 1987. Stock identification with the maximum-likelihood mixture model: sensitivity analysis and application to complex problems. Can. J. Fish. Aquat. Sci. 44: 866-881.

Wood, C. C., D. T. Rutherford, and S. McKinnell. 1989. Identification of sockeye salmon (*Oncorhynchus nerka*) stocks in mixed-stock fisheries in British Columbia and Southeast Alaska using biological markers. Can. J. Fish. Aquat. Sci. 46: 2108-2120.

Wright, S. 1965. The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution 19: 395-420.

Table 1. Summary of sockeye salmon collections from coastal populations.

Region	Lake	Pop. No.	Year	Date	Number sampled for: Hypural Length	Sex	Otoliths	Scales	Brain Parasite	Tissue Electrophoresis
Queen Charlotte Islands (statistical areas 162)	Eden L.	1a	1982	Sep. 27 - 28	100	150	50	100*	50	50
		b	1983	Oct. 5	0	0	0	0	26	26
	Awun L.	2	1982	Sep. 28	0	48	50	50	50	0
	Mercer L.	3a	1982	Sep. 25	90	140	50	50*	50	50
		b	1983	Sep. 13	100	100	100	100	100	100
	Yakoun L.	4a	1982	Sep. 27 - 28	100	149	50	100	50	50
		b	1989	Sep. 22	81	81	81	81	81	81
	Skidegate L.	5a	1982	Oct. 15 - 18	0	28	28	28	28	0
		b	1989	Oct.	49	49	49	49	49	49
	Mathers L.	6	1982	Sep. 24	110	160	50	160	50	50
North (statistical areas 5-7)	Border L.	7	1987	Sep. 3	50	50	0	50	49	49
	Lowe L.	8	1986	Sep. 28	93	93	93	93	93	93
	Bonilla L.	9	1983	Aug. 3	0	50	50	50*	100	100
	Devon L.	10	1985	Sep. 10 - 11	100	100	100	100	100	100
	Mikado L.	11	1986	Oct. 9	100	100	100	100	100	100
	Banks L.	12	1986	Oct. 4 - 5	100	100	100	100	100	100
	Kitlope L.	13	1986	Sep. 4	45	45	45	45	45	45
	Canoona L.	14	1986	Oct. 16 - 17	100	100	100	100	100	100
	Tankeeha L.	15	1986	Oct. 19	100	50	100	100	100	100
Central (statistical areas 8-10)	Kimsquit L.	16	1986	Nov. 5 - 6	84	84	84	84	84	84
	Tenas L.	17	1985	Oct. 2	100	100	100	100	100	100
	Koeye L.	18	1986	Oct. 3	100	100	100	100	100	100
	Owikeno L.	19a	1982	Sep. 15	100	100	0	100	50	100
		b	1984	Oct. 4	100	100	100	100	100	100
		c	1989	Oct. 9	100	100	100	100	100	100
	Long L.	20a	1982	Jul. 15	85	85	0	100	100	84
		b	1984	Oct. 3	154	154	154	154	100	100
		c	1989	Oct. 9	100	100	100	100	100	100
South (statistical areas 11-24)	Moss L.	21	1985	Oct. 23	100	100	100	100	100	100
	Sakinaw L.	22	1988	Nov.	0	0	0	10	83	83
	Great Central L.	23a	1983	Jun. 21-Sep. 13	1008	1008	993	993*	1008	143
		b	1990	Aug. 9 - 30	100	100	100	100	100	100
	Sproat L.	24a	1983	Jun. 14-Sep. 8	1125	1125	1125	1125*	1125	183
		b	1990	Sep. 14	50	50	50	50	50	50
	Kennedy L.	25a	1980	Sep. 3	0	0	0	0	81	0
		25b	1986	Nov. 21	91	91	91	91	91	91
	Henderson L.	26	1983	Oct. 6 - 18	299	299	299	299*	299	154
	Nobiton L.	27	1987	Nov. 17	100	100	100	100	100	100
	Cheewhat L.	28	1984	Oct. 11	100	100	100	100	100	100

*Additional scales collected in other years for scale pattern measurements.

Table 2. Enzymes and tissues used to investigate genetic variation. Tissues: E, eye; H, heart; L, liver; M, sleletal muscle. Buffers: AC, amine citrate (Clayton and Tretiak 1972); RW, Tris, citric acid, lithium hydroxide, and boric acid (Ridgway et al. 1970); MF, Tris, boric acid, EDTA, pH 8.5 (Markert and Faulhaber 1965).

Enzyme	Tissue	Locus	Buffer
Aspartate aminotransferase	H	*sAAT-1,2**	AC
	E	*sAAT-3**	AC
Adenosine deaminase	M	*ADA-2**	AC
Aconitate hydratase	L	*sAH-3**	AC
Alanine aminotransferase	M	*ALAT**	MF
Glyceraldehyde-3-phosphate dehydrogenase	E	*GAPDH-4,5**	AC
Glycerol-3-phosphate dehydrogenase	M	*G3PDH-1**	AC
Glucose-6-phosphate dehydrogenase	M	*G6PDH**	AC
Glucose-6-phosphate isomerase	M	*GPI-1,2,**	MF
L-Iditol dehydrogenase	L	*IDDH**	RW
Isocitrate dehydrogenase (NADP+)	M	*sIDHP-1,2**	AC
	L	*sIDHP-3,4**	AC
L-Lactate dehydrogenase	M	*LDH-A,B**	MF
	H	*LDH-C**	AC
	L	*LDH-D**	RW
	E	*LDH-E**	MF
Malate dehydrogenase	L	*sMDH-1,2**	AC
	M	*sMDH-3,4**	AC
Malic enzyme (NADP+)	M	*MEP-1,**	AC
Mannose-6-phosphate isomerase	H	*MPI**	AC
Dipeptidase	E	*PEPA**	MF
Phosphoglucomutase	H	*PGM-1**	AC
	M	*PGM-2**	MF
Superoxide dismutase	L	*sSOD**	RW

Table 3. Age distribution by sample for adult sockeye salmon collections. Age was determined from both scales and otoliths.

Pop.			No.	Proportion of Fish in each age class (number in parentheses)							
No.	Location	Year	aged	0.2	0.3	1.1	1.2	1.3	2.1	2.2	2.3
1	Eden L.	1982	46	0	0	0	0.65(30)	0.11(5)	0.02(9)	0.20(9)	0.02(1)
2	Awun L.	1982	50	0	0	0	0.72(36)	0.26(13)	0	0.02(1)	0
3	Mercer L.	1982	49	0	0	0.02(1)	0.29(14)	0.22(11)	0.06(3)	0.10(5)	0.31(15)
		1983	99	0	0	0.03(3)	0.02(2)	0.38(38)	0.01(1)	0.10(10)	0.45(45)
4	Yakoun	1982	49	0	0	0.08(4)	0.68(34)	0.22(11)	0	0	0
		1989	78	0	0	0.01(1)	0.36(28)	0.60(47)	0	0.03(2)	0
5	Skidegate L.	1982	26	0	0	0.23(6)	0.42(11)	0.04(1)	0	0.31(8)	0
		1989	49	0	0	0.04(2)	0.51(25)	0	0.04(2)	0.41(20)	0
6	Mathers L.	1982	42	0	0	0.02(1)	0.40(17)	0.07(3)	0.05(2)	0.36(15)	0.10(4)
8	Lowe L.	1986	92	0	0	0	0.33(30)	0.63(58)	0	0.01(1)	0.03(3)
9	Bonilla L.	1983	50	0	0	0	0.66(33)	0.24(12)	0	0.10(5)	0
10	Devon L.	1985	99	0	0	0	0.17(17)	0.65(64)	0	0.01(1)	0.17(17)
11	Mikado L.	1986	91	0	0	0.08(7)	0.29(26)	0.03(3)	0.09(8)	0.48(44)	0.03(3)
12	Banks L.	1986	98	0	0	0	0.68(67)	0.07(7)	0.03(3)	0.21(21)	0
13	Kitlope L.	1986	38	0.03(1)	0.03(1)	0.03(1)	0.55(21)	0.32(12)	0	0.05(2)	0
14	Canoona L.	1986	96	0	0	0	0.80(77)	0.01(1)	0	0.19(18)	0
15	Tankeeah L.	1986	99	0	0	0.18(18)	0.75(74)	0	0.05(5)	0.02(2)	0
16	Kimsquit L	1986	78	0	0	0.13(10)	0.56(44)	0	0.13(10)	0.18(14)	0
17	Tenas L.	1985	98	0	0.01(1)	0.02(2)	0.55(54)	0.38(37)	0	0.01(1)	0.03(3)
18	Koeye L.	1985	100	0	0	0.04(4)	0.58(58)	0.35(35)	0	0.01(1)	0.02(2)
19	Owikeno L.	1984	92	0	0	0	0.72(66)	0.27(25)	0	0.01(1)	0
		1989	96	0	0.01(1)	0	0.56(54)	0.42(40)	0	0	0.01(1)
20	Long L.	1984	131	0.04(5)	0	0	0.54(71)	0.38(50)	0	0.03(4)	0.02(2)
		1989	100	0	0	0	0.79(79)	0.21(21)	0	0	0
21	Moss L.	1985	98	0	0	0	0.63(62)	0.37(36)	0	0	0
23	Great Central L.	1983	938	0	0	0.02(21)	0.64(598)	0.29(271)	0.00(3)	0.02(16)	0.03(29)
		1990	96	0	0	0.24(23)	0.19(18)	0.27(26)	0.06(6)	0.22(22)	0.01(1)
24	Sproat L.	1983	1094	0	0	0.06(66)	0.63(686)	0.27(297)	0.01(9)	0.02(25)	0.01(11)
		1990	50	0	0	0.16(8)	0.58(29)	0.24(12)	0	0.02(1)	0
25	Kennedy L.	1986	88	0	0	0.01(1)	0.43(38)	0.56(49)	0	0	0
26	Henderson L.	1983	296	0	0	0.01(2)	0.32(96)	0.66(196)	0	0.00(1)	0.00(1)
27	Hobiton L.	1987	97	0	0	0.05(5)	0.91(88)	0.01(1)	0	0.03(3)	0
28	Cheewhat L.	1984	99	0	0	0.38(38)	0.53(52)	0	0.01(1)	0.08(8)	0

Table 4. Mean post-orbital hypural length (mm) by sex and age (1.2 and 1.3 only) for spawning sockeye collected from sampling areas. Standard deviations in parentheses.

			Males				Females			
			Age 1.3		Age 1.2		Age 1.3		Age 1.2	
Pop. No.	Location	Yr	N	Mean hypural length	N	Mean hypural length	N	Mean hypural length	N	Mean hypural length
1	Eden L.	82*	23	442(27.5)	-	- -	45	432(23.2)	-	- -
3	Mercer L.	83	17	472(15.4)	0	- -	21	460(16.2)	2	475(7.1)
4	Yakoun L.	82*	42	405(35.4)	-	- -	28	404(30.5)	-	- -
		89	19	456(26.1)	12	390(36.7)	28	463(19.0)	16	448(40.3)
5	Skidegate L.	89	0	- -	18	378(25.3)	0	- -	7	350(21.4)
6	Mathers L.	82*	46	393(39.5)	-	- -	52	403(18.6)	-	- -
7	Border L.	87*	27	502(39.6)	-	- -	18	487(39.3)	-	- -
8	Lowe L.	86	35	561(20.2)	21	544(38.7)	23	549(17.1)	9	541(37.8)
10	Devon L.	85	46	483(22.6)	15	425(19.2)	18	484(25.7)	2	430(00.0)
11	Mikado L.	86	3	494(11.0)	17	442(32.2)	0	- -	9	440(25.7)
12	Banks L.	86	4	515(22.1)	48	444(28.0)	3	470(28.6)	19	436(25.8)
13	Kitlope L.	86	10	530(28.5)	18	425(53.0)	2	523(05.0)	3	463(84.9)
14	Canoona L.	86	1	436(-)	20	435(18.6)	0	- -	57	434(27.5)
15	Tankeeah L.	86	0	- -	31	438(23.6)	0	- -	7	441(24.1)
16	Kimsquit L.	86	0	- -	17	504(23.2)	0	- -	27	478(14.4)
17	Tenas	85	19	465(28.4)	37	391(26.8)	18	451(14.2)	17	393(30.5)
18	Koeye L.	85	22	463(22.4)	37	420(25.0)	13	444(38.5)	21	415(37.3)
19	Owikeno L.	82*	45	507(45.3)	-	- -	32	514(18.7)	-	- -
		84	10	475(41.2)	47	428(41.2)	15	488(13.7)	19	452(32.3)
		89	27	449(38.3)	44	431(33.7)	14	485(14.5)	10	423(27.9)
20	Long L.	82	20	516(27.2)	11	454(27.3)	42	510(18.4)	2	460(7.1)
		84	35	495(29.2)	56	435(26.0)	15	478(30.5)	15	426(18.8)
		89	9	473(30.7)	40	421(27.4)	12	493(33.2)	39	425(15.1)
21	Woss L.	85	23	465(25.4)	44	434(21.0)	13	449(19.0)	18	429(38.6)
23	Great Central	83	120	502(25.0)	287	441(25.5)	151	486(20.7)	311	429(20.9)
		90	5	484(35.1)	13	423(25.2)	21	474(28.2)	5	401(20.1)
24	Sproat L.	83	141	501(25.2)	224	441(25.6)	156	484(25.9)	462	424(23.9)
		90	7	499(30.5)	19	418(28.4)	5	494(21.3)	10	408(21.9)
25	Kennedy L.	86	29	492(27.0)	17	458(25.1)	20	471(20.6)	21	449(38.5)
26	Henderson L.	83	103	487(24.8)	57	436(22.2)	93	479(18.4)	39	433(18.8)
27	Hobiton L.	87	1	425(-)	61	383(27.5)	0	- -	27	395(13.4)
28	Cheewhat L.	84	0	- -	40	367(31.4)	0	- -	12	378(31.5)

* sea age unknown because otoliths were not collected and scales were resorbed

Table 5. Sex composition of spawning sockeye salmon by sample location.

Pop. No.	Location	Year	Proportion female (No. in parentheses)
1	Eden L.	1982	0.67 (101)
2	Awun L.	1982	0.27 (48)
3	Mercer L.	1982	0.64 (89)
		1983	0.66 (66)
4	Yakoun	1982	0.44 (66)
		1989	0.58 (47)
5	Skidegate L.	1982	0.25 (7)
		1989	0.26 (13)
6	Mathers L.	1982	0.56 (89)
7	Border L.	1987	0.44 (22)
8	Lowe L.	1986	0.38 (35)
9	Bonilla L.	1983	0.30 (15)
10	Devon L.	1985	0.26 (26)
11	Mikado L.	1986	0.38 (38)
12	Banks L.	1986	0.31 (31)
13	Kitlope L.	1986	0.16 (7)
14	Canoona L.	1986	0.76 (76)
15	Tankeeah L.	1986	0.16 (8)
16	Kimsquit L	1986	0.49 (42)
17	Tenas L.	1985	0.37 (37)
18	Koeye L.	1985	0.40 (40)
19	Owikeno L.	1982	0.52 (52)
		1984	0.39 (39)
		1989	0.25 (25)
20	Long L.	1982	0.60 (52)
		1984	0.25 (38)
		1989	0.51 (51)
21	Woss L.	1985	0.33 (33)
23	Great Central L.	1983	0.51 (502)
		1990	0.40 (40)
24	Sproat L.	1983	0.59 (673)
		1990	0.30 (15)
25	Kennedy L.	1986	0.46 (42)
26	Henderson L.	1983	0.45 (299)
27	Hobiton L.	1987	0.34 (34)
28	Cheewhat L.	1984	0.14 (14)

Table 6. Mean number of circuli and incremental distances (mm x 100) in scale zones of age 1.2 sockeye salmon. Standard deviations are given in parentheses.

Pop No.	Location	Year	n	NC_1(SD)	NC_2(SD)	NC_3(SD)	ID_1(SD)	ID_2(SD)	ID_3(SD)
1	Eden L.	1980	25	13.44(1.53)	2.08(0.70)	31.20(3.06)	32.68(4.07)	4.09(1.62)	125.73(14.21)
3	Mercer L.	1979*	7	10.43(1.51)	2.14(1.86)	29.29(0.76)	26.35(1.66)	3.96(3.21)	111.54(11.65)
8	Lowe L.	1986	17	10.41(1.73)	1.47(0.72)	31.59(2.55)	30.35(3.09)	2.88(1.31)	108.48(10.96)
9	Bonilla L.	1981*	41	9.56(1.80)	1.63(0.70)	31.97(3.07)	25.48(5.04)	2.88(1.26)	119.83(14.14)
10	Devon L.	1985	14	12.43(1.83)	1.29(0.47)	35.11(2.67)	31.20(4.25)	2.36(0.86)	122.67(8.45)
11	Mikado L.	1986	15	11.67(2.13)	2.33(0.72)	29.78(2.05)	28.02(4.58)	4.43(1.51)	105.21(9.20)
12	Banks L.	1986	33	11.97(1.31)	4.88(1.80)	29.63(2.41)	31.20(3.88)	10.81(4.16)	111.47(13.02)
13	Kitlope L.	1986	14	13.64(2.10)	2.31(0.95)	36.71(3.59)	31.13(5.46)	4.26(1.55)	104.19(10.41)
14	Canoona L.	1986	48	12.92(2.21)	1.63(0.07)	27.26(3.14)	35.83(5.54)	3.30(1.44)	93.39(13.50)
15	Tankeeah L.	1986	58	14.40(1.96)	1.76(1.01)	30.56(3.28)	34.69(5.11)	3.57(2.22)	112.03(13.80)
16	Kimsquit L	1986	27	9.44(2.04)	2.78(1.12)	29.19(3.08)	25.50(4.95)	5.79(2.69)	92.53(11.64)
17	Tenas L.	1985	30	9.73(1.36)	2.00(0.95)	28.58(2.72)	25.88(4.03)	3.96(2.03)	84.14(8.71)
18	Koeye L.	1985	13	6.62(1.26)	3.77(2.05)	31.62(2.43)	18.25(2.86)	8.48(5.65)	100.14(8.54)
19	Owikeno L.	1984	31	8.62(1.44)	2.55(1.06)	32.36(3.21)	19.86(3.50)	4.72(2.15)	104.69(13.78)
20	Long L.	1984	41	8.81(1.57)	2.22(0.91)	32.46(2.98)	22.10(3.38)	4.76(2.27)	109.23(10.01)
21	Woss L.	1985	38	8.67(0.99)	1.18(0.39)	31.14(2.98)	23.51(3.38)	2.33(0.86)	98.56(9.99)
23	Great Central L.	1985*	51	10.12(1.42)	2.45(1.08)	31.20(3.25)	29.42(3.97)	5.09(2.38)	110.83(15.05)
24	Sproat L.	1985	52	11.71(1.93)	1.73(0.80)	32.21(3.31)	34.53(5.26)	3.39(1.64)	119.28(15.18)
25	Kennedy L.	1986*	26	6.77(1.31)	2.23(0.95)	31.23(3.42)	20.64(2.64)	4.75(2.09)	117.21(13.76)
26	Henderson L.	1984*	29	12.86(1.83)	1.31(0.54)	28.21(2.24)	37.47(6.02)	2.56(1.03)	104.51(9.73)
27	Hobiton L.	1987	57	10.35(1.93)	5,74(1.84)	30.34(3.73)	27.86(3.22)	11.81(4.74)	99.27(13.00)

*Brood year affected by lake enrichment

Table 7. Mean number of circuli and incremental distances (mm x 100) in scale zones of age 1.3 sockeye salmon. Standard deviations are given in parentheses.

Pop. No.	Location	Year	n	NC_1(SD)	NC_2(SD)	NC_3(SD)	ID_1(SD)	ID_2(SD)	ID_3(SD)
1	Eden L.	1980	30	13.57(1.72)	2.47(0.90)	29.57(3.66)	35.20(4.30)	5.21(2.43)	114.54(13.17)
3	Mercer L.	1979	7	11.29(2.43)	2.29(0.95)	28.00(2.45)	26.33(5.64)	4.34(2.16)	114.27(13.59)
8	Lowe L.	1986	30	11.43(1.48)	1.70(0.47)	31.30(2.35)	31.53(4.19)	3.14(1.08)	106.38(9.93)
9	Bonilla L.	1981	27	11.00(1.96)	1.56(0.75)	33.57(3.63)	26.98(4.61)	2.89(1.67)	125.18(13.77)
10	Devon L.	1985*	55	10.58(1.41)	1.44(0.60)	30.17(2.20)	29.82(3.15)	2.96(0.86)	114.36(9.64)
11	Mikado L.	1986	3	11.67(4.73)	2.33(0.58)	27.00(4.24)	26.38(6.40)	4.82(1.49)	108.92(11.53)
12	Banks L.	1986	3	12.67(2.31)	4.67(1.53)	27.00(2.83)	34.69(3.33)	10.47(4.16)	102.13(12.13)
13	Kitlope L.	1986	10	10.00(2.06)	2.90(0.99)	28.50(2.55)	28.19(6.39)	8.48(3.15)	84.02(6.63)
14	Canoona L.	1986	0						
15	Tankeeah L.	1986	0						
16	Kimsquit L	1986	0						
17	Tenas L.	1985	18	7.61(2.43)	1.39(0.70)	29.31(3.17)	24.27(3.45)	2.85(1.55)	91.38(11.72)
18	Koeye L.	1985	7	13.87(1.89)	2.27(1.22)	29.14(3.63)	34.72(4.61)	5.66(3.20)	115.51(10.29)
19	Owikeno L.	1984	15	8.40(2.06)	2.67(0.98)	28.67(3.81)	21.29(4.04)	6.40(2.66)	97.48(17.17)
20	Long L.	1984	35	8.34(1.19)	2.06(1.00)	29.00(2.29)	20.43(3.10)	4.17(2.02)	97.14(10.16)
21	Woss L.	1985	24	8.17(1.20)	1.50(0.59)	30.79(3.55)	19.83(3.25)	2.71(1.03)	97.53(12.30)
23	Great Central L.	1985*	38	12.42(1.84)	3.08(0.97)	28.68(3.07)	31.56(4.13)	6.92(2.32)	105.23(10.36)
24	Sproat L.	1985	35	11.17(1.90)	1.51(0.78)	32.03(2.62)	30.74(3.84)	2.90(1.63)	116.29(12.75)
25	Kennedy L.	1986*	22	9.05(1.46)	1.68(0.78)	32.23(2.54)	25.65(3.32)	3.81(1.82)	112.11(9.84)
26	Henderson L.	1984*	38	11.76(1.55)	1.26(0.50)	29.21(2.65)	31.14(5.46)	2.58(1.06)	104.90(12.23)
27	Hobiton L.	1987*	0						

*Brood year affected by lake enrichment

Table 8. Prevalence of the brain parasite *Myxobolus arcticus* in spawning sockeye salmon by sample location.

Pop. No.	Location	Year	Number examined	Number infected	Proportion infected
1	Eden L.	1982	50	48	0.96
		1983	26	26	1.00
2	Awun L.	1982	50	0	0.00
3	Mercer L.	1982	50	41	0.82
		1983	100	87	0.87
4	Yakoun L.	1982	50	0	0.00
		1989	81	0	0.00
5	Skidegate L.	1982	28	0	0.00
		1989	45	0	0.00
6	Mathers L.	1982	50	20	0.40
7	Border L.	1987	48	46	0.96
8	Lowe L.	1986	92	38	0.41
9	Bonilla L.	1983	100	100	1.00
10	Devon L.	1985	100	100	1.00
11	Mikado L.	1986	100	99	0.99
12	Banks L.	1986	100	100	1.00
13	Kitlope L.	1986	45	0	0.00
14	Canoona L.	1986	99	99	1.00
15	Tankeeah L.	1986	100	100	1.00
16	Kimsquit L	1986	84	0	0.00
17	Tenas L.	1985	100	96	0.96
18	Koeye L.	1985	100	98	0.98
19	Owikeno L.*	1982	50	50	1.00
		1984	100	99	0.99
		1989	100	99	0.99
20	Long L.*	1982	100	0	0.00
		1984	154	0	0.00
		1989	100	0	0.00
21	Woss L.	1985	100	55	0.55
22	Sakinaw L.	1988	83	67	0.81
23	Great Central L.*	1983	1008	25	0.02
		1990	100	18	0.18
24	Sproat L.*	1983	1125	1122	1.00
		1990	49	49	1.00
25	Kennedy L.	1980	81	79	0.98
		1986	91	90	0.99
26	Henderson L.*	1983	299	299	1.00
27	Hobiton L.	1987	99	99	1.00
28	Cheewhat L.	1989	100	98	0.98

*Data for additional years published in Quinn et al. (1987).

Table 9. Summary of allele frequencies by locus and sample.

LOCUS	POPULATION* 1a	1b	3a	3b	4a	4b	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19a	19b	19c	20a	20b	20c	21	22	23a	23b	24a	24b	25b	26	27	28
PGM-1*																																				
(N)	60	26	46	96	48	81	49	50	49	89	96	98	100	100	46	100	100	79	100	100	100	100	100	83	100	100	99	83	111	99	132	49	88	136	100	100
100	0.250	0.231	0.122	0.079	0.122	0.066	0.041	0.080	0.163	0.084	0.099	0.020	0.030	0.165	0.200	0.480	0.165	0.342	0.700	0.105	0.270	0.280	0.260	0.470	0.640	0.630	0.010	0.843	0.239	0.253	0.283	0.429	0.039	0.036	0.100	0.375
NULL	0.750	0.769	0.878	0.921	0.878	0.934	0.969	0.910	0.837	0.916	0.908	0.980	0.970	0.845	0.800	0.550	0.835	0.658	0.300	0.895	0.730	0.720	0.740	0.530	0.460	0.470	0.990	0.157	0.761	0.747	0.617	0.571	0.961	0.964	0.900	0.625
PGM-2*																																				
(N)	60	26	49	100	50	81	49	50	49	89	100	98	100	100	46	100	100	79	100	100	99	99	100	84	100	100	100	83	136	99	182	50	89	149	100	100
100	0.730	0.788	0.612	0.646	0.760	0.784	0.969	0.920	0.816	0.736	0.760	0.990	0.960	0.836	0.844	0.980	0.920	0.994	0.965	0.840	0.833	0.879	0.845	0.845	0.815	0.765	0.895	0.976	0.879	0.838	0.799	0.840	0.978	0.977	0.990	0.865
133	0.270	0.231	0.388	0.466	0.240	0.216	0.041	0.080	0.184	0.264	0.240	0.010	0.040	0.166	0.156	0.020	0.080	0.006	0.035	0.130	0.167	0.121	0.155	0.155	0.185	0.215	0.105	0.024	0.121	0.162	0.201	0.160	0.022	0.023	0.010	0.136
166	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
sMDH-3,4*																																				
(N)	60	26	50	100	50	81	49	50	49	92	100	100	100	100	46	100	100	80	100	100	99	100	100	84	100	102	100	83	143	100	180	50	91	124	100	99
100	1.000	0.962	1.000	0.990	0.990	1.000	1.000	1.000	1.000	1.000	0.990	0.995	0.990	0.936	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.990	0.966	1.000	1.000	0.976	0.975	0.992	1.000	1.000	0.960	0.995	0.995
66	0.000	0.038	0.000	0.010	0.010	0.000	0.000	0.000	0.000	0.000	0.010	0.005	0.010	0.064	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.034	0.000	0.000	0.024	0.025	0.008	0.000	0.000	0.040	0.005	0.005
108	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
GPI-1,2*																																				
(N)	60	24	47	87	44	81	49	47	49	90	94	90	100	100	39	100	100	79	96	98	93	100	100	84	82	100	97	83	76	100	128	50	90	111	98	99
100	0.970	0.979	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.986	1.000	1.000
FAST	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.014	0.000	0.000
SLOW	0.030	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
MEP-1*																																				
(N)	60	26	49	100	50	81	49	50	49	92	100	100	99	100	42	100	100	80	99	98	100	100	100	84	100	100	100	83	136	100	183	50	91	164	100	99
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.995	0.995	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.995	0.990	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
63	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
G6PDH*																																				
(N)	60	26	50	100	50	81	49	50	49	92	100	98	100	100	46	100	100	81	100	100	93	100	100	84	100	100	100	83	136	100	183	50	91	104	100	99
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.916	0.900	0.880	0.881	1.000	1.000	0.986	1.000
94	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.085	0.100	0.120	0.000	0.000	0.015	0.000	
G3PDH-1*																																				
(N)	29	20	29	100	49	81	49	28	49	92	100	100	100	100	46	100	100	80	98	99	97	99	100	84	98	100	99	83	136	100	183	50	91	164	98	99
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
sMDH-1,2*																																				
(N)	60	26	50	100	50	81	49	50	49	92	100	100	100	100	46	100	100	81	100	96	96	100	100	84	98	99	100	83	143	100	183	50	91	164	100	100
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.995	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
147	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
LDH-B*																																				
(N)	60	26	49	100	50	81	48	49	49	92	98	100	100	100	46	100	100	81	100	100	100	100	100	84	100	100	100	83	143	100	183	50	91	164	100	100
100	0.990	1.000	0.602	0.646	1.000	1.000	1.000	1.000	0.959	1.000	0.844	0.970	1.000	0.936	0.988	1.000	0.966	1.000	0.940	0.996	0.960	0.980	0.975	0.994	0.980	0.986	1.000	1.000	1.000	0.997	1.000	1.000	1.000	1.000	1.000	
116	0.010	0.000	0.398	0.336	0.000	0.000	0.000	0.000	0.041	0.000	0.066	0.030	0.000	0.046	0.011	0.000	0.046	0.000	0.066	0.004	0.040	0.020	0.025	0.006	0.020	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
86	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
LDH-C*																																				
(N)	60	26	49	100	50	81	48	49	49	89	40	100	100	100	46	100	100	79	100	100	100	100	100	83	98	100	100	83	114	99	168	50	91	164	99	100
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
FAST	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
sIDHP-3,4*																																				
(N)	60	26	47	100	50	80	49	50	49	92	100	100	100	100	46	100	100	81	100	98	100	96	99	84	100	100	100	83	143	100	183	50	91	164	97	96
100	0.960	0.981	0.979	1.000	1.000	0.994	1.000	0.990	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.984	0.990	1.000	1.000	1.000	1.000	1.000	0.979	0.990	1.000	1.000	1.000	1.000	0.969	0.922
FAST	0.040	0.019	0.021	0.000	0.000	0.006	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.016	0.010	0.000	0.000	0.000	0.000	0.000	0.021	0.010	0.000	0.000	0.000	0.000	0.031	0.078
MPI*																																				
(N)	40	26	48	100	41	81	49	49	49	89	0	97	100	100	46	100	100	79	100	100	100	99	100	84	99	100	100	83	92	99	93	50	91	113	100	100
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	-	0.933	0.906	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
96	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-	0.067	0.094	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
LDH-C*																																				
(N)	46	26	49	97	22	80	49	48	0	90	0	99	100	98	46	100	100	81	98	100	99	97	99	81	99	100	100	83	143	100	182	50	90	144	99	79
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	-	1.000	-	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.970	1.000	1.000	1.000	1.000	1.000
SLOW	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-	0.000	-	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.000	0.000	0.000	0.000	0.000
sAAT-1,2*																																				
(N)	0	0	0	0	0	81	49	0	49	89	0	100	100	100	46	100	100	79	100	100	0	100	100	0	100	100	98	83	0	99	0	50	91	0	98	100
100	-	-	-	-	-	1.000	1.000	-	1.000	1.000	-	1.000	0.996	0.996	1.000	1.000	0.995	1.000	1.000	1.000	-	1.000	1.000	-	1.000	1.000	1.000	1.000	-	0.996	-	1.000	1.000	-	1.000	1.000
83	-	-	-	-	-	0.000	0.000	-	0.000	0.000	-	0.000	0.004	0.004	0.000	0.000	0.005	0.000	0.000	0.000	-	0.000	0.000	-	0.000	0.000	0.000	0.000	-	0.004	-	0.000	0.000	-	0.000	0.000
ADA-1*																																				
(N)	0	0	0	0	0	81	49	0	49	92	0	100	100	100	46	100	100	80	97	99	0	98	100	0	99	100	100	83	0	100	0	50	91	0	68	99
100	-	-	-	-	-	1.000	1.000	-	1.000	1.000	-	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	-	1.000	0.966	-	1.000	0.975	1.000	1.000	-	0.970	1.000	-	1.000	1.000	-	1.000	1.000
94	-	-	-	-	-	0.000	0.000	-	0.000	0.000	-	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	-	0.000	0.046	-	0.000	0.025	0.000	0.000	-	0.030	-	0.000	0.000	-	0.000	0.000
sIDHP-1,2*																																				
(N)	0	0	0	0	0	81	49	0	49	90	0	100	100	100	46	100	100	81	100	100	0	99	100	0	100	100	99	83	0	100	0	50	91	0	100	99
100	-	-	-	-	-	1.000	1.000	-	1.000	1.000	-	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	-	1.000	1.000	-	1.000	1.000	1.000	1.000	-	1.000	-	1.000	1.000	-	1.000	1.000
LDH-A,B*																																				
(N)	0	0	0	0	0	81	48	0	49	92	0	98	100	100	46	100	100	81	98	100	0	100	100	0	96	100	99	83	0	100	0	50	91	0	100	100
100	-	-	-	-	-	1.000	1.000	-	1.000	1.000	-	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	-	1.000	1.000	-	1.000	1.000	1.000	1.000	-	1.000	-	1.000	1.000	-	1.000	1.000

| | | |

Fig. 1. Location of coastal sockeye populations sampled.

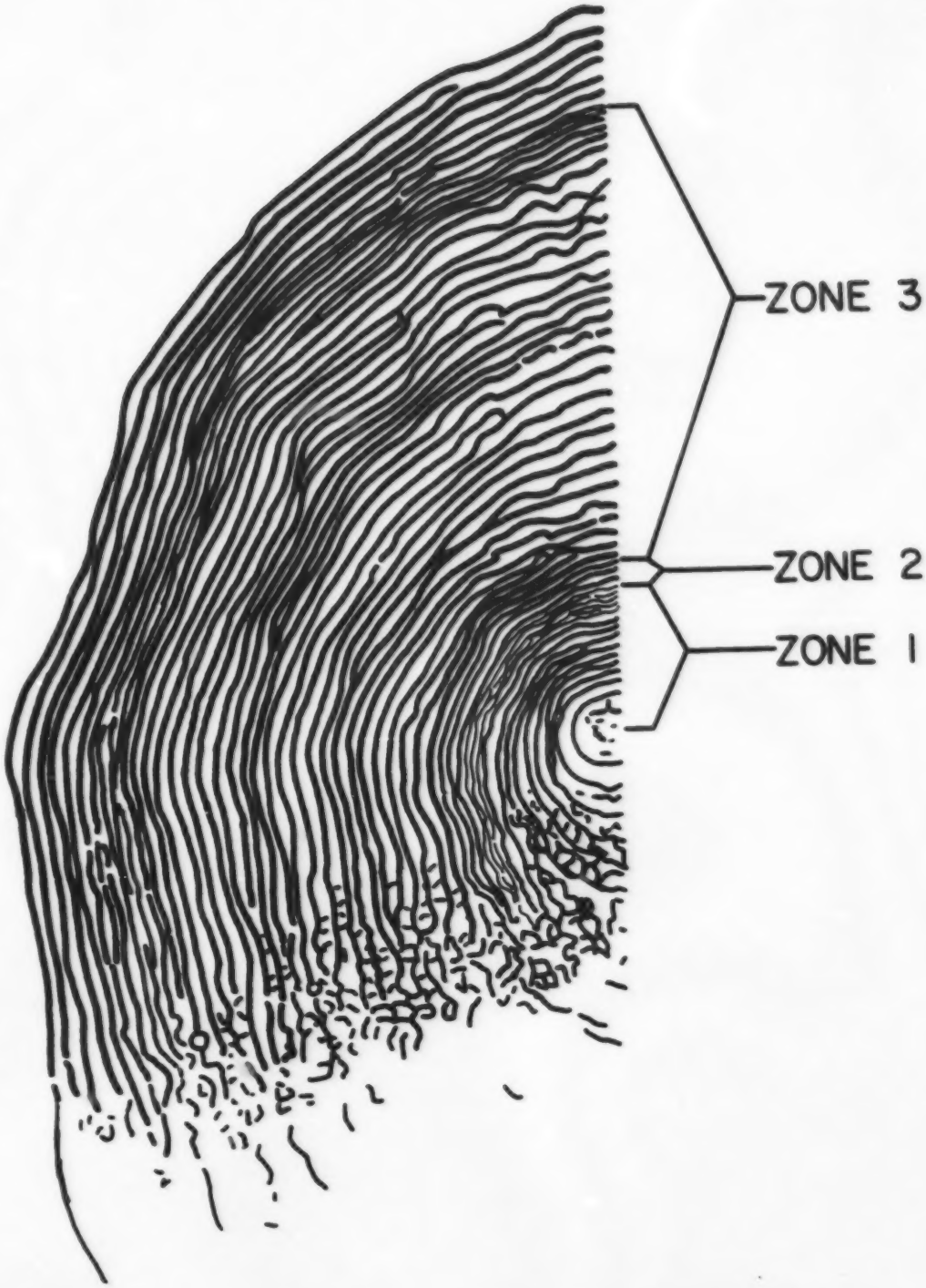


Fig. 2. Diagram of a typical sockeye salmon scale explaining growth zone definitions for age 1.2 and 1.3 fish.

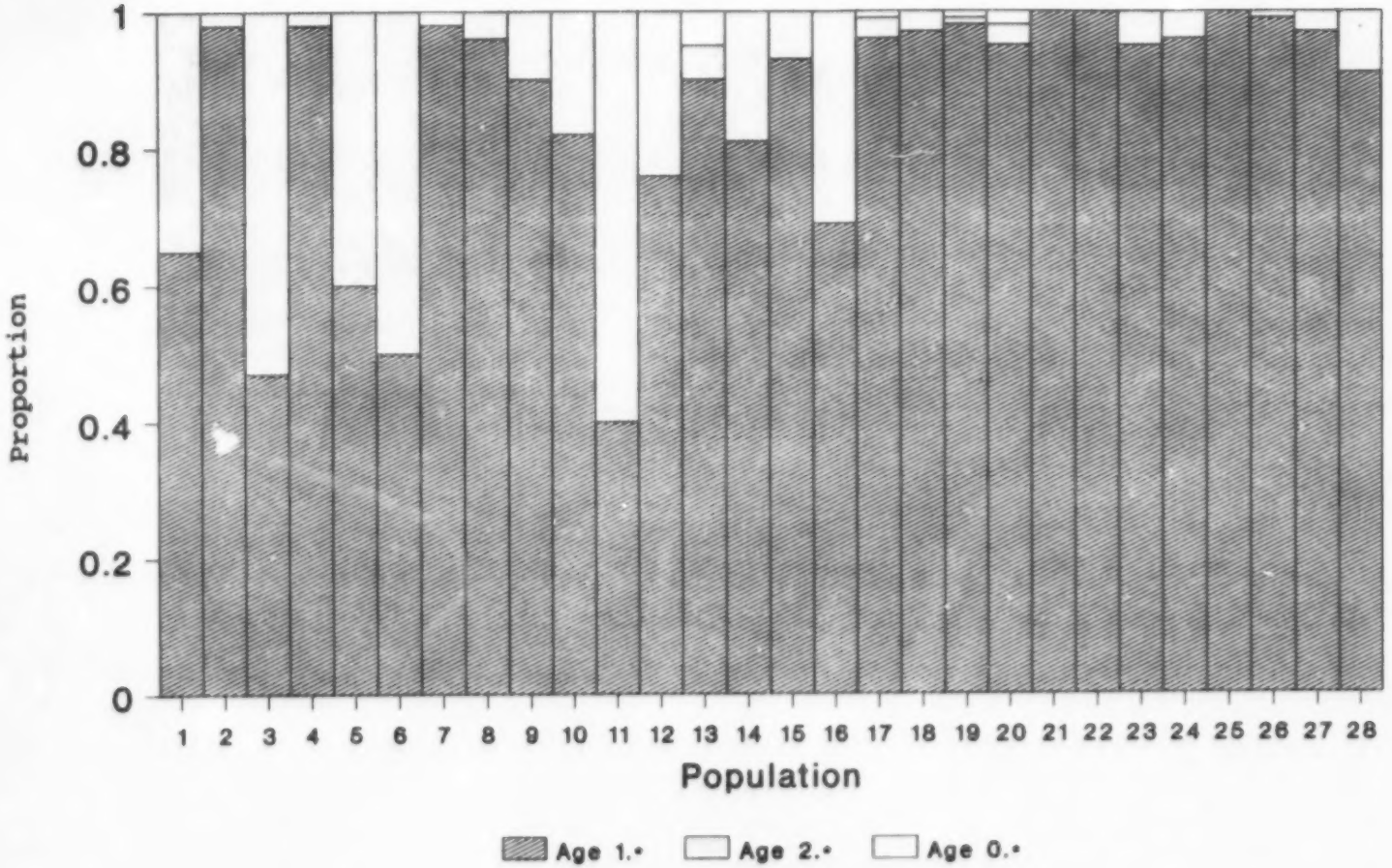


Fig. 3. Variation in freshwater age composition among coastal sockeye populations. Replicate samples from multiple years were pooled.

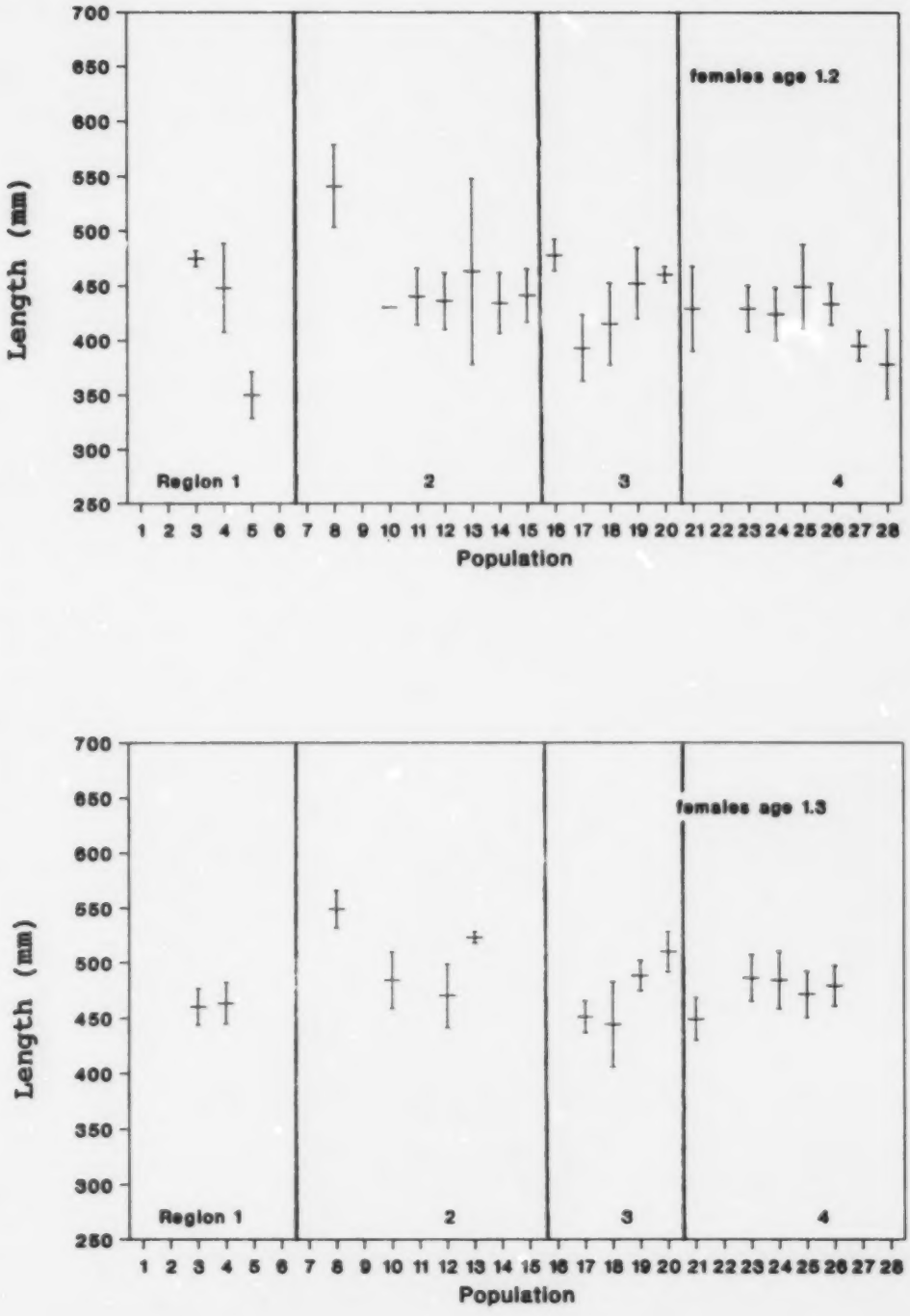


Fig. 4A. Variation in mean post-orbital hypural length (± one standard deviation) among coastal sockeye populations. Replicate samples from multiple years were pooled.
(A) spawning females; (B) spawning males.

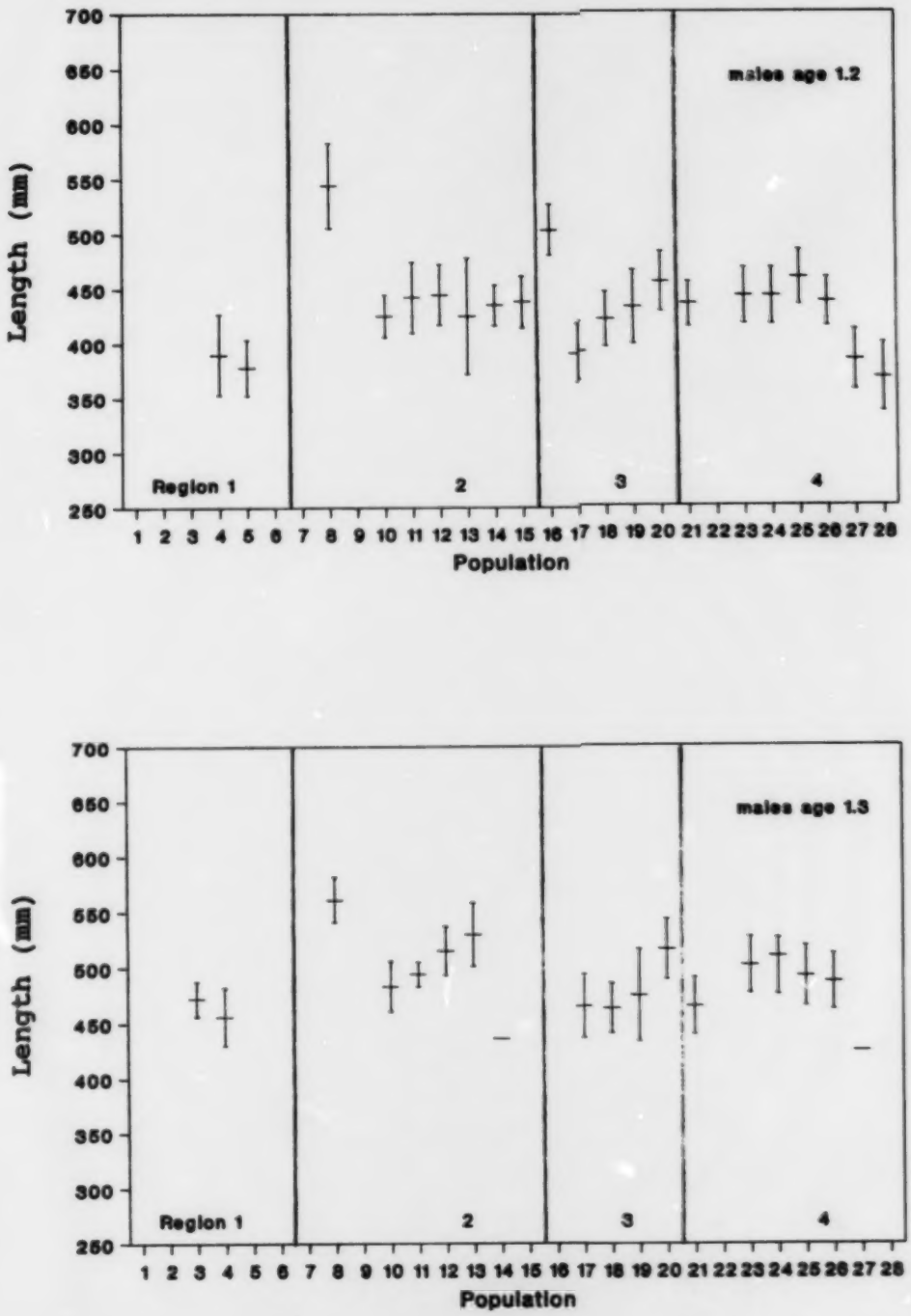
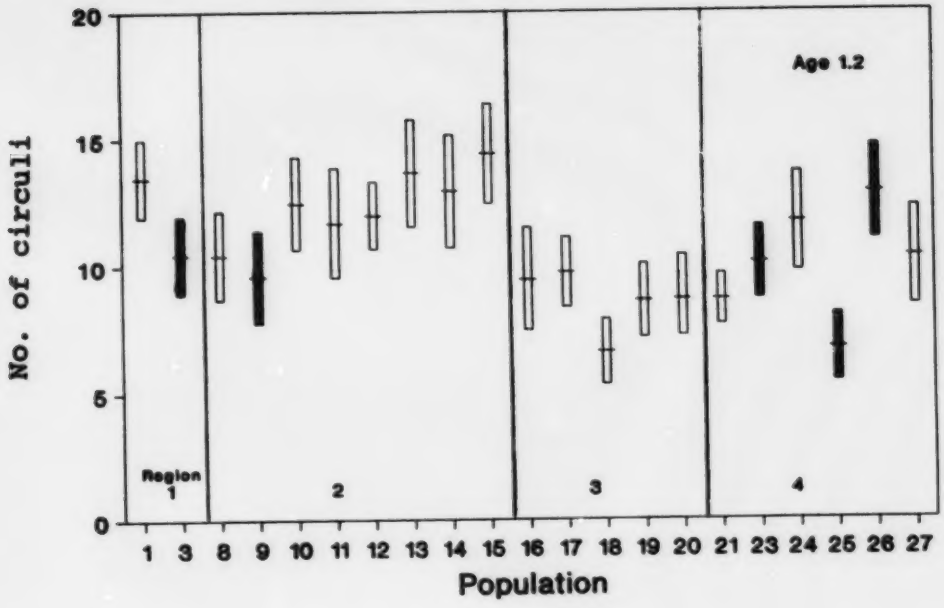


Fig. 4B. Variation in mean post-orbital hypural length (± one standard deviation) among coastal sockeye populations. Replicate samples from multiple years were pooled.
(A) spawning females; (B) spawning males.



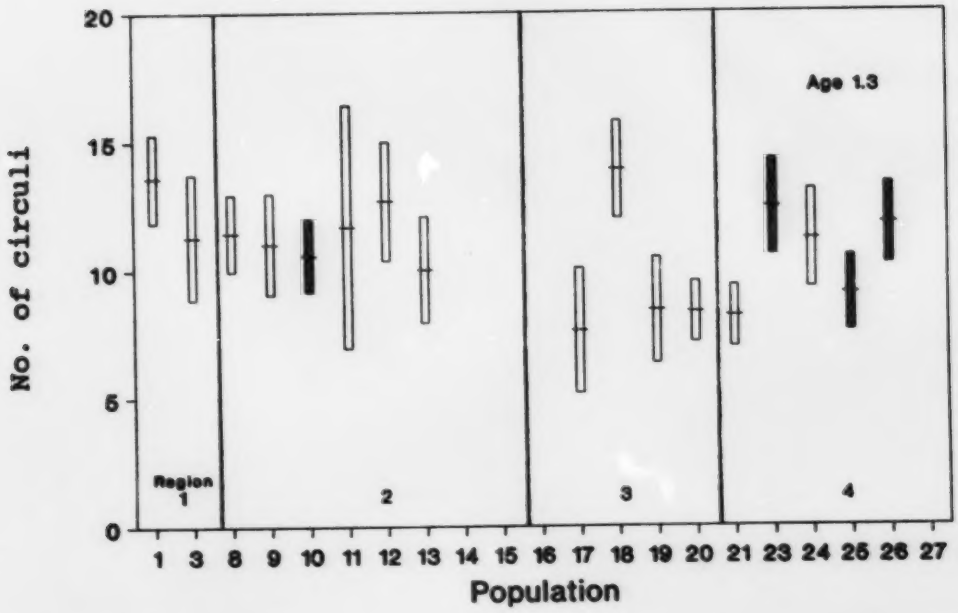
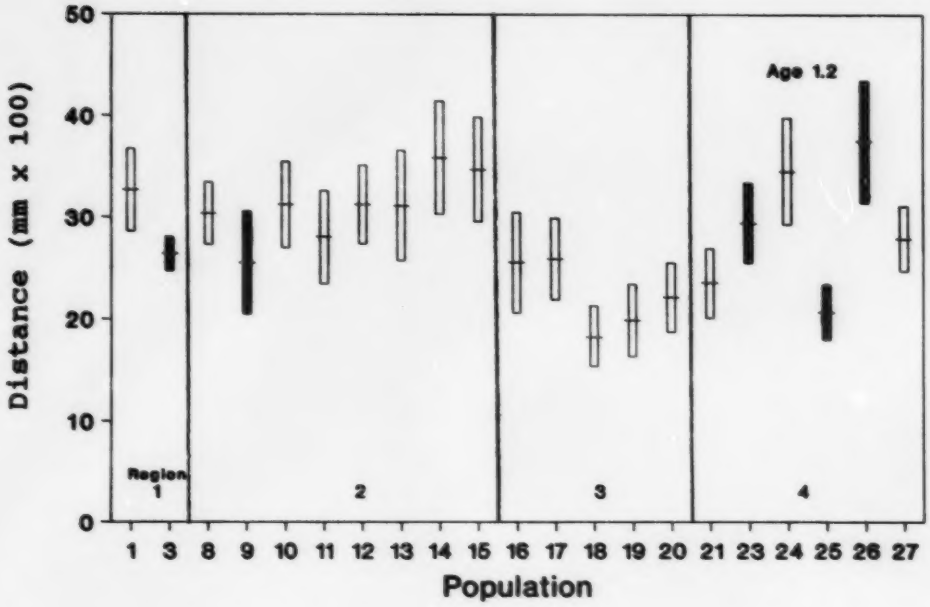


Fig. 5A. Variation in mean scale pattern variables (± one standard deviation) among coastal sockeye populations. Measurements taken from Zone 1 of scales from spawning fish. Solid bars indicate samples from brood years affected by lake enrichment.
(A) circulus counts; (B) incremental distances.



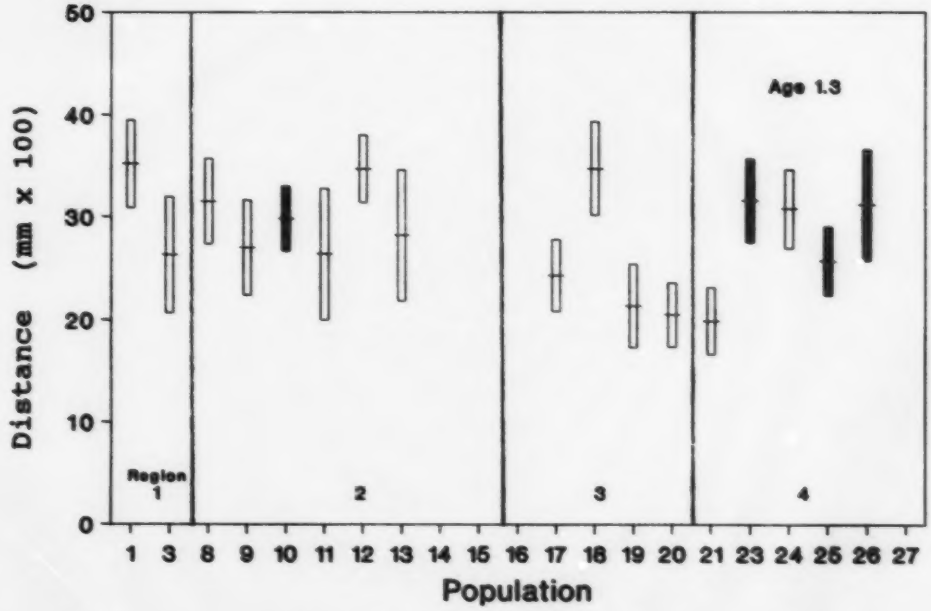


Fig. 5B. Variation in mean scale pattern variables (± one standard deviation) among coastal sockeye populations. Measurements taken from Zone 1 of scales from spawning fish. Solid bars indicate samples from brood years affected by lake enrichment.
(A) circulus counts; (B) incremental distances.

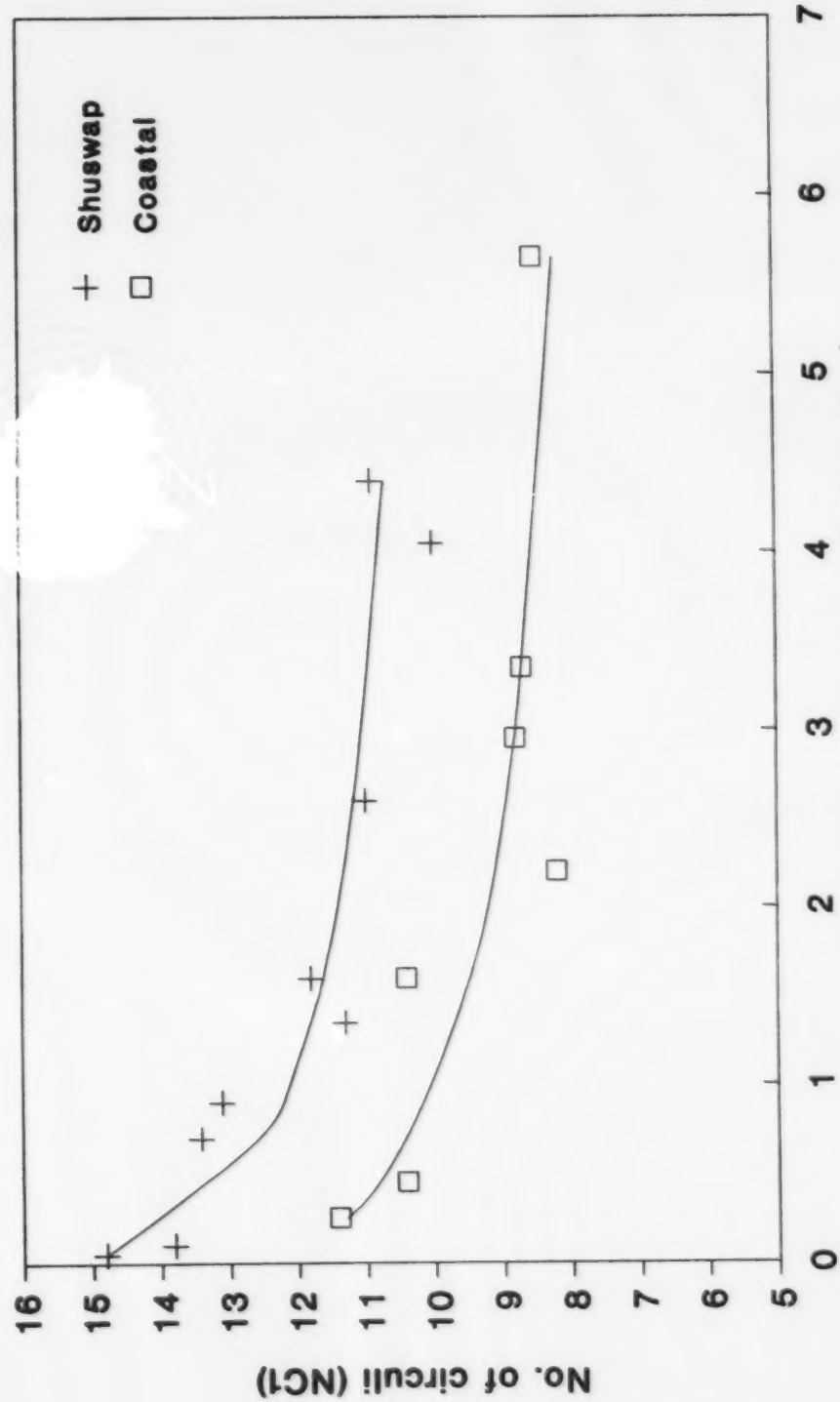


Fig. 6. Comparison of the relationship between circulus counts in scale Zone 1 and limnetic fish density for coastal and interior sockeye populations.

Fig. 7. Prevalence of Myxobolus arcticus in coastal sockeye populations. Dark area of pie diagram indicates proportion of fish infected. Replicate samples from multiple years were pooled.

Fig. 8. Similarity dendrogram for coastal sockeye populations based on Nei's unbiased genetic identity (Nei 1978) and allele frequencies at *PGM-1**, *PGM-2**, *sMDH-3,4**, *GPI-1,2**, *MEP-1**, *G6PDH**, *G3PDH**, *sMDH-1,2**, *LDH-C**, *LDH-D**, *sIDHP-3,4**.

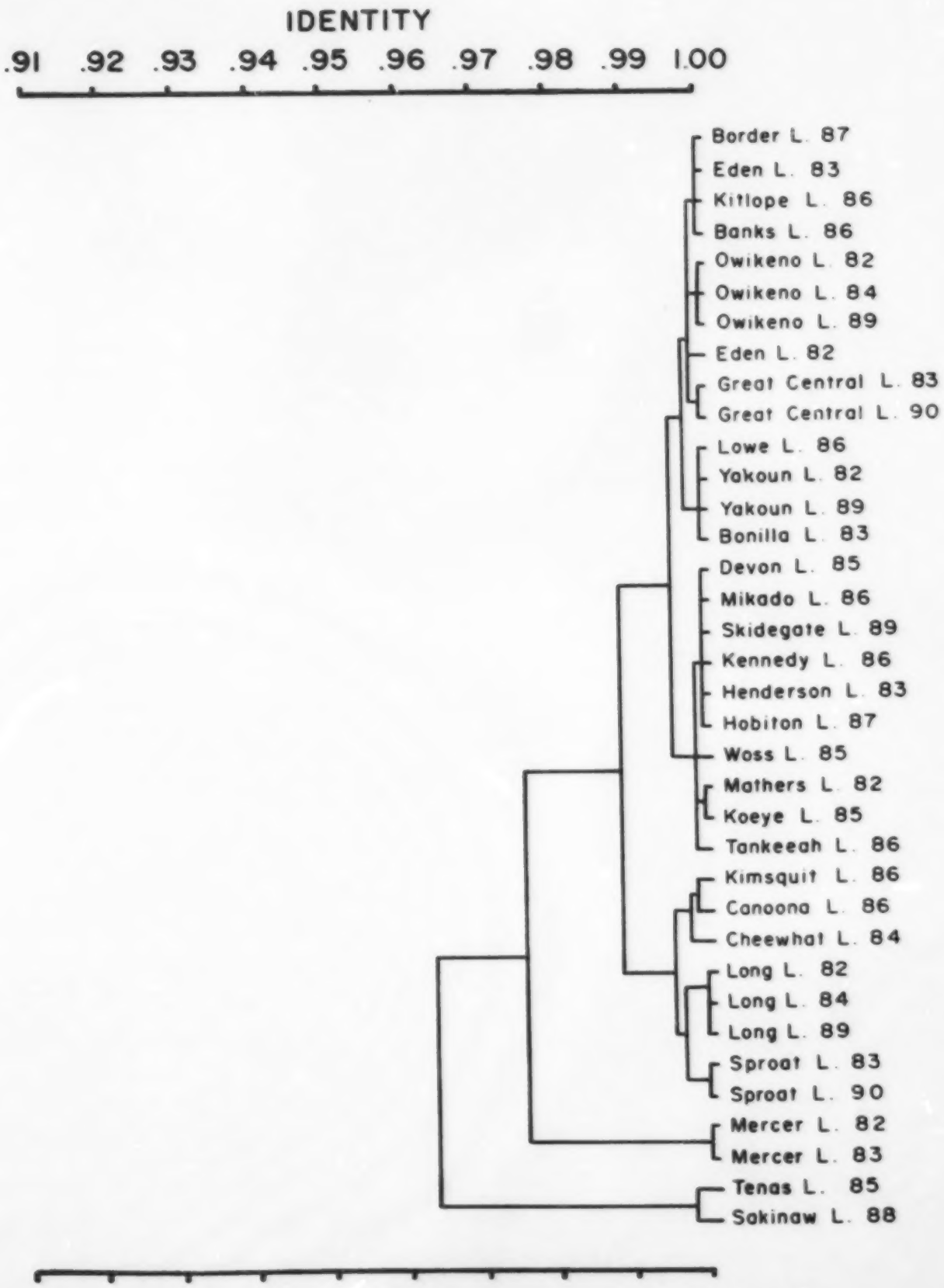
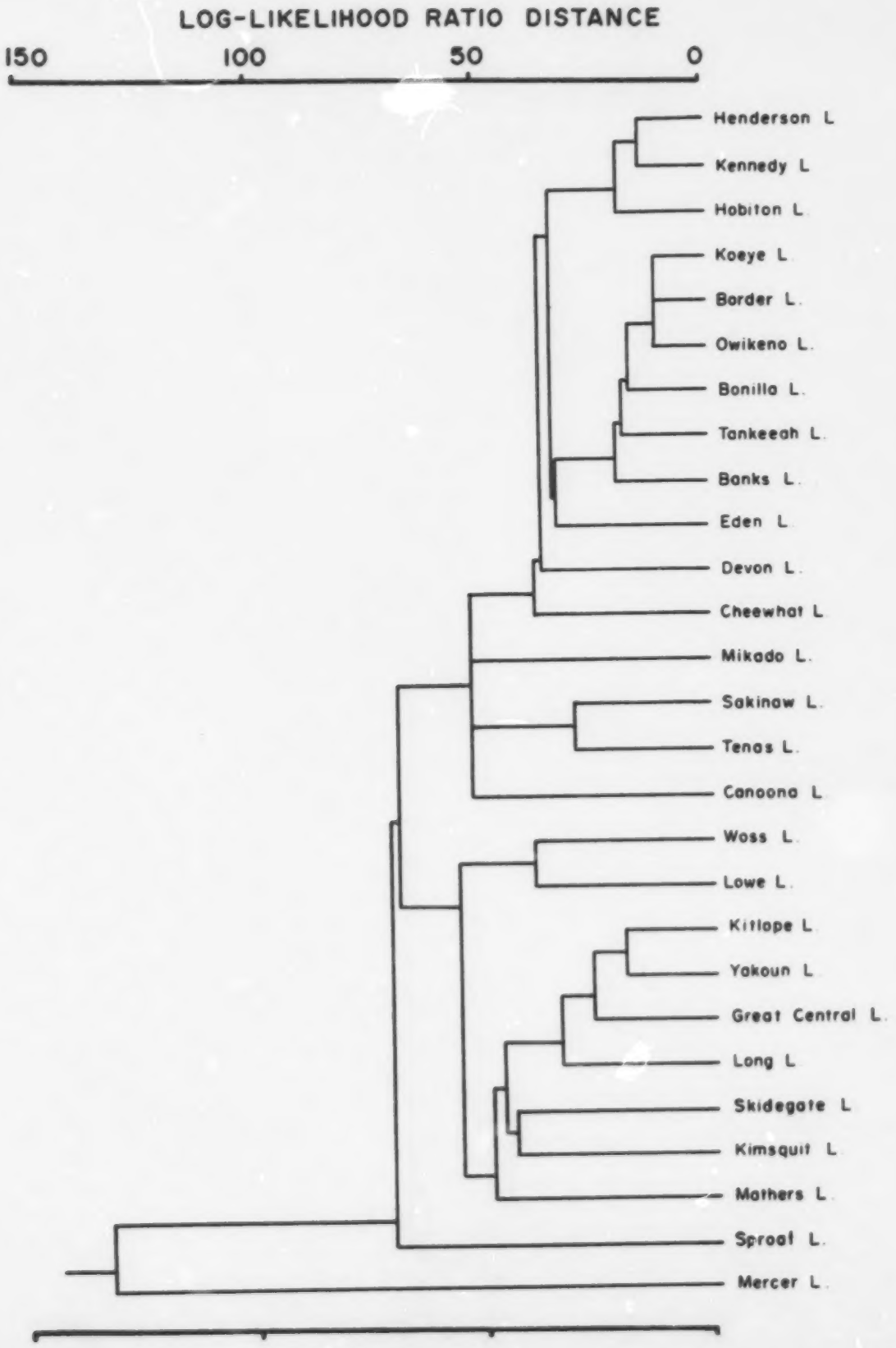

IDENTITY
.91
.92
.93
.94
.95
.96
.97
.98
.99
1.00
Border L. 87
Eden L. 83
Kitlope L. 86
Banks L. 86
Owikeno L. 82
Owikeno L. 84
Owikeno L. 89
Eden L. 82
Great Central L. 83
Great Central L. 90
Lowe L. 86
Yakoun L. 82
Yakoun L. 89
Bonilla L. 83
Devon L. 85
Mikado L. 86
Skidegate L. 89
Kennedy L. 86
Henderson L. 83
Hobiton L. 87
Woss L. 85
Mathers L. 82
Koeye L. 85
Tankeeah L. 86
Kimsquit L. 86
Canoona L. 86
Cheewhat L. 84
Long L. 82
Long L. 84
Long L. 89
Sproat L. 83
Sproat L. 90
Mercer L. 82
Mercer L. 83
Tenas L. 85
Sakinaw L. 88

Fig. 9. Similarity dendrogram illustrating the potential for differentiating coastal sockeye populations using genetic, parasite, and age composition data in combination. The log likelihood ratio distance (Wood 1989) reflects the cumulative differences among populations in allele frequencies at the five most polymorphic loci (*PGM-1**, *PGN-2**, *sMDH-3,4**, *LDH-D**, *sIDHP-3,4**), in the prevalence of the brain parasite *Myxobolus arcticus* and in freshwater age composition.


LOG-LIKELIHOOD RATIO DISTANCE
150
100
50
0
Henderson L.
Kennedy L.
Hobiton L.
Koeye L.
Border L.
Owikeno L.
Bonilla L.
Tankeeah L.
Banks L.
Eden L.
Devon L.
Cheewhat L.
Mikado L.
Sakinaw L.
Tenas L.
Canoona L.
Woss L.
Lowe L.
Kitlope L.
Yakoun L.
Great Central L.
Long L.
Skidegate L.
Kimsquit L.
Mathers L.
Sproat L.
Mercer L.

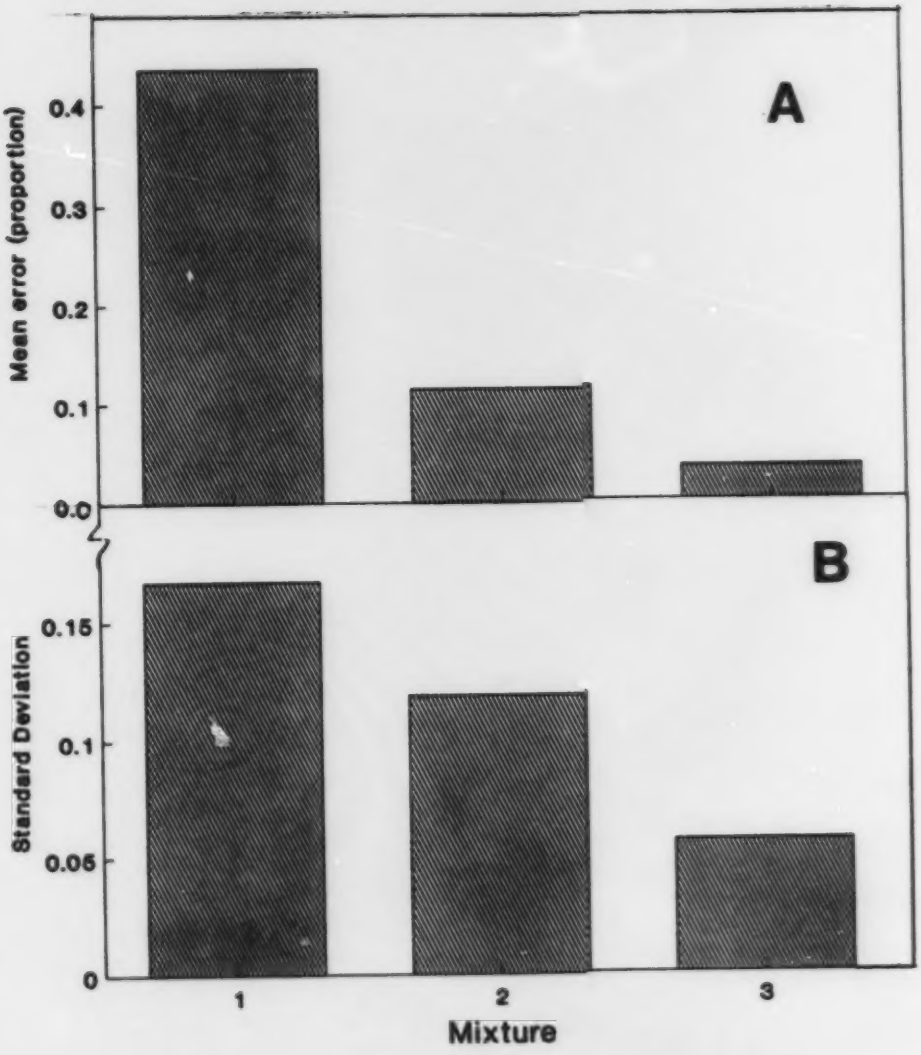


Fig. 10. Accuracy (A) and precision (B) of stock composition estimates for three test "mixtures" of coastal sockeye populations. Mixture 1 included 300 fish from Koeye Lake; mixture 2, 300 fish from Long Lake; and mixture 3, 300 fish from Mercer Lake. Test mixtures were resampled 100 times each. A mean error of 44% for test mixture 1 (for example) implies that in 100 trials, the average estimate of mixture composition was only 56% Koeye sockeye whereas the true composition was 100% Koeye sockeye.